SPATIAL MANAGEMENT STRATEGIES FOR DEEP-SEA SHARKS

by

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BSc

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Those who go down to the sea in ships, who do business on great waters; they have seen the works of the LORD, and his wonders in the deep. Psalm 107.

STAEMENTS AND DECLARATIONS

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Ross Kelvin Daley

Hobart, 15th of March, 2017

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LIST OF ABBREVIATIONS

AFMA	Australian Fisheries Management Authority
ANOVA	Analysis of variance
AIC	Akaike Information Criteria
Auto-longline	Automatically baited demersal longline [fishing method]
CMR	Commonwealth Marine Reserve
DUR	Duration [of tag detection]
DI	Detection index
DNA	Deoxyribonucleic acid
DUR	Duration
DVM	Diel vertical migration
EDF	Effective degrees of freedom
EPBC	Environment Protection and Biodiversity Conservation
f	Fishing mortality
FL	Fork length
GAMM	Generalized Additive linear Mixed-effects Model
GHAT	Gillnet Hook and Trap [sector of the SESSF]
IBM	Individual based model
ICES	International Convention for Exploration of the Sea
IUCN	International Union for the Conservation of Nature
k	Growth parameter of the VBGM
km	kilometer
m	Natural mortality
MLD	Maximum linear distance
MS	Mid-continental slope: 650–1200 m
MSE	Management Strategy Evaluation
Mt	Mitochondrial (DNA)
N days	Number of days [that a tagged shark was detected]
OTLF	Ocean Trap and Line Fishery [of New South Wales]
SE	Standard error
SESSF	Southern and Eastern Scalefish and Shark Fishery
SET	Southeast Trawl [sector of the SESSF]
spp.	Species plural (more than one species from the same genus)
t	metric ton (1000 kilograms)
TAC	Total allowable catch
TL	Total length
USDMS	Upper-Slope Dogfish Management Strategy
US	Upper-continental slope: 200–650 m
VBGM	von Bertalanffy growth model 1938

ABSTRACT

At least ten species of deep-sea (> 200m) dogshark (Squaliformes) have undergone major declines in the world's Oceans due to historical over-fishing. Two species were recently protected in Australia (*Centrophorus harrissoni* and *C. zeehaani* (Centrophoridae)) and a recovery plan was implemented. The key strategies of this plan are landing bans to prevent targeted fishing and a network of areas closed to all methods of fishing. This is the first closure network to be implemented in the world specifically for the recovery of a vulnerable deep-sea species. Success will take decades because these species are long lived (30+ years) and have only 1–2 pups every three years and therefore remain vulnerable, even as bycatch.

This thesis develops and applies a novel combination of field based survey methods and model based approaches to support management of these sharks or other vulnerable vertebrates that co-occur with more productive fisheries target species. These include, developing biologically meaningful criteria to measure performance against the broad conservation objectives of the plan – "halt decline and support recovery", choosing appropriate locations and sizes for closures, understanding and limiting if possible the cost to industry due to lost fishery production, and improving monitoring and compliance data.

Three principal datasets are used: 1. Genetic taxonomy data for *Centrophorus* species, used to resolve identification issues in observer records so they can be used to ensure targeted fishing for *Centrophorus* in Australia has stopped, ensure estimates of fishing mortality are reliable, and ultimately monitor recovery from fishing vessels. 2. Survey data including abundance (catch and effort) and population structure (sex ratios and size structure), used to select suitable locations for closures and provide a baseline abundance estimate to measure recovery. 3. Passive acoustic tracking data, used to measure the home range of *C. zeehaani* to inform closure size.

The protected *Centrophorus* species are externally very similar to each other and some other non-protected *Centrophorus* species in Australia. My genetic approach found the 16S mitochondrial gene was able to distinguish six out of seven species from Australia and Indonesia. The remaining two species should not be confused because they occur in different geographic areas. The genetic identification method was tested on ten fin-clip samples provided by fishery observers and found all but one had been correctly identified by observers. This method will provide a means of non-lethal catch verification.

Passive acoustic tracking was used to study the movements of *C. zeehaani* in the largest closure implemented for their protection. An array of 21 moored acoustic receivers monitored 71tagged individuals for 15 months. A general additive mixed model was applied to the data to test environmental variables (mainly light) as fixed effects on shark movement and individual variation as a random effect. Average along-slope range was 19.2 ± 12.2 km and the maximum distance recorded was 75 km over 15 months. Average depths ranged from 340 m at night to 640 m during the day with high individual variation. Detection depth was strongly correlated with seafloor depth. These results indicate a distinct daily movement pattern of synchronous diel migration with (night time ascent). Males tended to leave the closure and most did not return whereas the number of females detected did not vary significantly between months. The management implication of these results is that closures for *C. zeehaani* need to be 19–75 km in size along the upper-slope, cover the 340–640 m depth range and be located to protect resident females.

A semi-quantitative management strategy evaluation (MSE) approach was developed and applied to *C. harrissoni* and *C. zeehaani* to identify and evaluate options for closures at the local and national scales, particularly outside the range of the telemetry data. Population structure (survey) data were used to identify areas where mating and pupping was likely to occur as leading criteria for locating closures. Commonwealth fisheries managers chose options that added new closures to the network and expanded some existing closures even though costs to industry of lost production were high.

An individual-based simulation model of the movements of *C. zeehaani* was developed and applied to determine how long a depleted population would take to recover from its current status of 8% of un-fished numbers to a target of 20%. Individual movement patterns were based on tracking results and simulated across a spatial domain of three closures and fished areas with three different types of fishing gear and conditions. Key uncertainties were length of the female breeding cycle, natural mortality rate and spatial variation in population density. The base case (three year cycle, 2% natural mortality and survey based spatial variation in abundance) predicted recovery in 63 ± 3 years. Poor matching of closure locations to population density would delay recovery by an additional 31.9 years. Sensitivity testing predicted that the target would be reached 19.2 years earlier with a 2-year female breeding cycle or 16.5 years later with a four-year cycle. If natural mortality were half the base case estimate then the recovery target would be reached 13.5 years earlier or, significantly, if the natural mortality rate were double the base case estimate, recovery to the target would take 98.3 years longer than the base case.

Improving handling practices for sharks or changing fishing methods on the continental shelf would not significantly affect the time for recovery but re-introducing trawling for orange roughy (*Hoplostethus atlanticus*) in deep waters would delay recovery by 45.9 years. Doubling the size of a closure where *C. zeehaani* is abundant would reduce recovery time by 9.9 years; halving closure size there would increase recovery time by 12.6 years. Such changes would have no significant effects where *C. zeehaani* is not abundant. The model can be used to evaluate the consequences of alternative management interventions and the risks associated with key uncertainties and can be applied to other shark species with telemetry data.

Australia has implemented the first detailed recovery plan for a deep-sea species with spatial management as a key strategy. Decision makers were faced with conflicting conservation and resource use objectives and significant scientific uncertainties. This thesis has calculated the appropriate size of closures using linear models applied to telemetry data. Suitable locations for other closures were identified using demographic criteria developed from survey data. Population trends were simulated across the geographic range of a population over decades. Results of this thesis indicate that these species can be conserved but only with high costs of lost fishery production. Recovery will take decades, at least. The methods can be applied to plan conservation interventions for other long-lived deep-sea species.

CHAPTER 1. GENERAL INTRODUCTION

Most of this thesis focuses on Harrisson's Dogfish (*Centrophorus harrissoni*) and Southern Dogfish (*C. zeehaani*), as a case study in using spatial management strategies for recovery of vulnerable deep-sea sharks. These species were chosen as the first deep-sea shark species in the world to be protected by a nation, mainly by areas closed to fishing. This chapter starts by providing much broader descriptions of diversity and life history of deep-sea sharks. These descriptions highlight the range of deep-sea sharks, the biogeographic factors that make some species particularly vulnerable, and how breeding drives individual movements. A brief description of the ecology of Australia's continental slope follows highlighting causes of high endemism and restricted habitat. Trophic ecology is also described briefly as a potential driver of feeding movements. The history of fishery impacts and conservation measures in Australia show how quickly these species can be depleted and how some control measures have not worked. This chapter ends by taking a pragmatic look at how shark tagging methods and tag data analysis can be matched to the practical challenges of spatial management, leading to research objectives.

1.1 Diversity

There are many species of cartilaginous fishes (chondrichthyans) with low biological productivity and high exposure to fishing that are likely to emerge as issues in the world's oceans. The Class Chondrichthyes contains 1144 formally described species from the world's oceans (W.T. White, CSIRO personal communication). Of these, 530 species are considered to occur primarily in the deep sea (Kyne and Simpfendorfer 2010). For the purposes of this study, deep-sea species refers to those that occur primarily outside the 200 m bathymetric contour, which separates the continental shelf from the continental slope. Just under half of deep-sea chondrichthyans (254 species) are sharks (members of the Subclass Elasmobranchii with gill openings on the side of the head). The remaining species are batoids (elasmobranches with gill openings on the ventral surface) and chimaeras (members of the Subclass Holocephali). This thesis is focused on deep-sea sharks because the batoids and chimaeras have very little data in fisheries making the effects of fishing difficult to study.

Most deep-sea sharks (85%) are from two taxonomic groups: the squaloid dogsharks (Order Squaliformes, seven families) and the scyliorhinid catsharks (Order Carcharhiniformes, family Scyliorhinidae) (Kyne and Simpfendorfer 2010). Dogsharks can be distinguished from other chondrichthyan groups by the absence of an anal fin (Daley, Stevens *et al.* 2002; Last and Stevens 2009) (Figures 1.1, 1.2). Typical dogsharks have two dorsal fins with spines at

the anterior margin. Most species are less that 2m in length, although one family, the sleeper sharks (Somniosidae), grow up to 4 m (Compagno, Dando *et al.* 2005). Dogsharks are by far the most taxonomically diverse group of deep-sea sharks with seven families inhabiting all the world's oceans (Compagno, Dando *et al.* 2005). Off Australia the group contains 49 species including representatives of all seven families and at least 12 endemic species (Last and Stevens 2009) (Table 1.1).

Catsharks can be distinguished from other shark families in having an anal fin and two dorsal fins that are well behind the origin of the pelvic-fin origin (Last and Stevens 2009) (Figure 1.1). All are less than 2 m long (Compagno, Dando *et al.* 2005; Kyne and Simpfendorfer 2010). Seven deep-sea species occur in Australian waters, six are endemic; the remaining species is restricted to the Southwestern Pacific (Last and Stevens 2009).

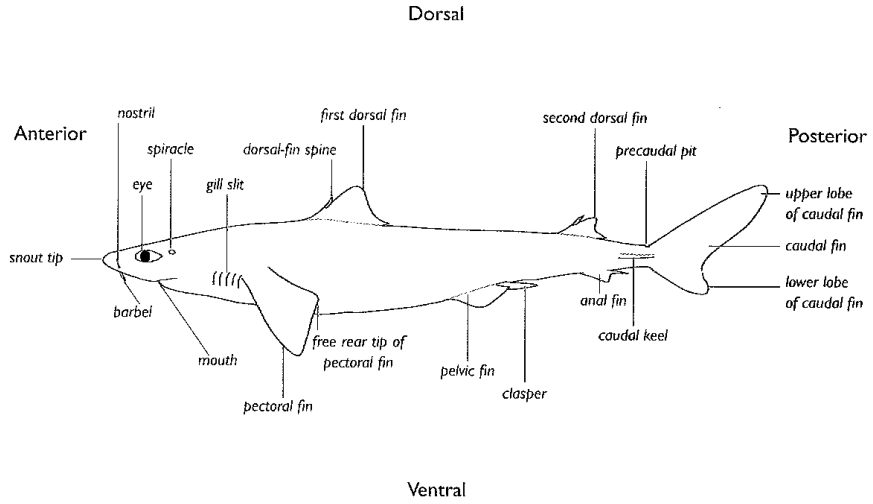
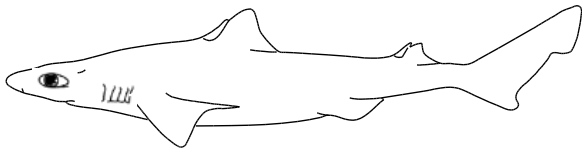
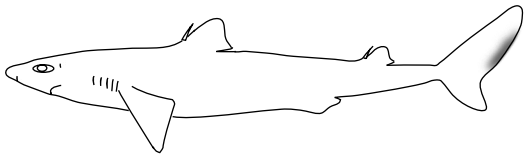


Figure 1.1 Anatomical features of a generalised shark (Daley 2002).

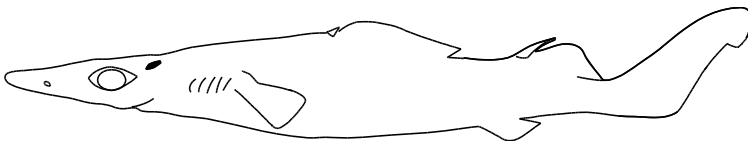
A few species of deep-sea shark are pelagic but most are demersal, that is living mainly within 50 m of the seafloor, even though the water column can be up to 1500 m deep (Table 1.1). The demersal species can be broadly divided into two ecological groups based on seafloor (bathymetric) depth range: upper-continental slope bathome (200–650 m) and mid-continental slope bathome (650–1200 m) (Daley, Stevens *et al.* 2002; Pethybridge, Daley *et al.* 2010). These groups have some general ecological differences that are described in the following section.



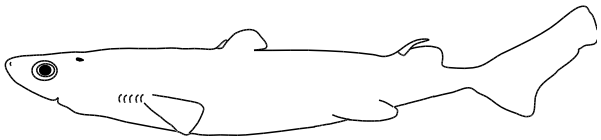
a) *Centrophorus zeehaani* (Centrophoridae), US, 45–96 cm TL.



b) *Squalus chloroculus* (Squalidae), US, up to 99 cm TL.



c) *Deania calcea* (Centrophoridae), MS, 30–122 cm TL.



d) *Etmopterus granulosus* (Etmopteridae), MS, 20–65 cm TL.

Figure 1.2 Example deep-sea dogsharks (Order Squaliformes) from Australian waters. US=upper-slope demersal (200–650 m), MS=mid-slope demersal (>650 m). Size range indicates size at birth (where known)–maximum adult total length (TL).

Table 1.1 Diversity among demersal deep-sea sharks from Australian waters

Family, Genus and species	Risk Status	Bathome	Adult TL (cm)
DOGSHARKS			
Centrophoridae (gulper sharks)			
Centrophorus seven species e.g. *C. zeehaani* (Figure 1.2a)	*C. harrissoni* endangered	US	70–170
Deania calcea (Figure 1.2c), *D. quadrispinosa*		MS	75–122
Dalatiidae (kitefin sharks)			
Dalatias licha	Near threatened	MS	100–60
Isistius brasiliensis, I. plutodus	Least concern, data deficient	P	40–50
Echinorhinidae (bramble sharks)			
Echinorhinus brucus, E. cookei	Data deficient, near threatened	US/MS	150–400
Etmoperidae (lantern sharks)			
Centroscyllium kamoharai	Data deficient	MS	44–63
Etmoperus 11 species e.g. *E. granulosus* (Figure 1.2d)	Data deficient, least concern	US/MS	24–90
Oxynotidae (prickly dogfishes)			
Oxynotus bruniensis	Data deficient	US	60–90
Somniosidae (sleeper sharks)			
Centroscymnus coelolepis, C. owstoni	Near threatened, Least concern	MS	70–122
Centroselachus crepidater	Least, concern	MS	80–105
Proscymnodon plunketi	Near threatened	MS	110–170
Scymnodalatias albicaudata, S. sherwoodi	Data deficient	US/P	74–110
Somniosus antarcticus	Data deficient	MS	400–456
Zameus squamulosus	Data deficient	US/P	47–84
Squalidae (dogfishes)			
Cirrhigaleus australis	Data deficient	US	–123
Squalus (11 species) e.g. *S. chloroculus* (Figure 1.2 b)	Near threatened, Data deficient	US	46–91
CATSHARKS			
Scyliorhinidae (catsharks)			
Apristurus (8 species)	Most species Data deficient	MS	47–87
Bythaelurus incanus	Data deficient	MS	–45
Cephaloscyllium (7 species)	Near threatened, Data deficient	US	30–110
Figaro boardmani, F. striatus	Least concern, Data deficient	US	38-–61

US=upper-slope demersal (200-650 m), MS=mid-slope demersal (>650 m), P=pelagic (Last and Stevens 2009). TL= total length.

Risk status based on classification by the International Union for the Conservation of Nature (IUCN 2016).

1.2 Life history

Understanding reproduction, age and growth are essential for population assessment models. They also help us to understand why many deep-sea sharks are vulnerable and which attributes make some species particularly so.

Shark reproduction differs from bony fish in that fertilization is internal. This means mating, and birth/egg laying can be separated in space and time. This promotes movement between habitats that are more suitable for pups or adults, to find conditions to promote growth, or avoid predation. Depending on the species, females have one of two reproductive modes: oviparous (egg layers) or viviparous (live bearers). In oviparous mode, the fertilized ova are encased in a leathery shell to form eggs that pass quickly through the uteri and are then laid in pairs onto the seafloor. In viviparous mode the fertilized ova develop within the uteri into embryos that are born live (Hamlett and Koob 1999). Oviparous shark species include the catsharks (Awruch, Pankhurst *et al.* 2009). Most other chondrichthyans, including the dogsharks are viviparous (Braccini, Hamlett *et al.* 2007; Graham and Daley 2011).

Generally viviparous species are considered to have lower reproductive output than viviparous species and are more likely to be at risk to fishing (Daley, Knuckey *et al.* 2007; Daley, Webb *et al.* 2007). Most deep-sea shark species lack distinct breeding seasons, unlike their relatives from the continental shelf. This has been attributed to a more stable environment, less influenced by the seasonal light and temperature signals that affect surface waters (Wetherbee 1996). The lack of seasonality makes it difficult to calculate reproductive output directly but the number of years in the female cycle can be determined from embryo size classes (Braccini, Gillanders *et al.* 2006; McLaughlin and Morrissey 2005)

A variety of methods are used for aging sharks. Some rely on counting annuli in calcified cartilage, analogous to counting the rings in a tree (McAuley, Simpfendorfer *et al.* 2006). Most dogsharks have vertebrae that are poorly calcified and are instead aged by counting bands on the dorsal spines. Most species in this group show a general pattern of long life with late maturity; Females tend to grow older and larger and males. For example female *C. crepidater* live up to 54 years on the mid-slope of southeastern Australia (Irvine, Stevens *et al.* 2006b). In some dogshark families, lifespan has been linked to size. For example in the Etmopteridae, smaller species (<30 cm) such as *Etmopterus spinax* lives to only 9 years in of the north-east Atlantic Ocean (Gennari and Scacco 2007) whereas the Giant Lantershark *E. baxteri*, grows up to 90 cm and lives to 57 years around southeastern Australia (Irvine,

Stevens *et al.* 2006a). There is a complete lack of knowledge of age and growth for any deep-sea catsharks, which have poorly calcified vertebrae and no spines.

A range of models have been used to model the age and growth rates of deep-sea sharks; most commonly the von Bertalanffy (1938) growth model (VBGM) (Campana 2001). The three key parameters represent length at birth ($L0$), maximum length ($L\infty$) and growth rate (k) – the rate at which the maximum length is approached. The VBGM also has some weaknesses and doesn't always provide a good fit (Haddon 2001). In particular the parameters $L0$ and $L\infty$ are highly influenced by very large and very small individuals that are mainly outside the range of most of the data collected for two reasons. Firstly, very few individuals in a population reach maximum size (Sainsbury 1980). Secondly juveniles often escape sampling nets because they are smaller than the mesh size.

Population assessment of deep-sea sharks needs to be spatially explicit. Dogsharks in particular segregate by sex, size, maturity and reproductive stage (Moura, Jones *et al.* 2014; Yano and Tanaka 1988). These patterns can be further complicated by seasonal changes in the distribution of different demographic components (males, females, juveniles) and complex patterns of movement associated with mating and recruitment (Veríssimo, McDowell *et al.* 2011). Upper-slope examples include *C. harrissoni* and *C. zeehaani*, which segregate by sex and maturity stage (Graham and Daley 2011). Mid-slope dogsharks including species of *Deania*, *Etmopterus* and *Centroscymnus* show similar geographic segregation that is further complicated by segregation across bathymetric depths (Moura, Jones *et al.* 2014) Even among mature individuals within the sexes there appears to be further segregation by reproductive stage (Girard and Du Buit 1999).

A number of reasons have been put forward to explain segregation patterns in sharks. These include protecting the young from predation by males, differences in dietary requirements, lack of ability by juveniles to catch active prey, or different metabolic requirements during pregnancy (Braccini, Gillanders *et al.* 2005; Sims 2003; Springer 1967).

1.3 Australian continental slope ecology

The water columns of Australia's upper and mid-slope bathomes differ substantially. The water mass from the surface to approximately 650m below the surface, that includes the demersal waters of the upper-slope, is affected by major boundary currents that contribute to geographic and seasonal variation in water temperature and salinity: the East Australian Current, Zeehaan Current, Flinders Current and Leeuwin Current (Harris, Nilsson *et al.* 1987; Koslow, Kloser *et al.* 1997; Prince 2001). This variation coincides with greater levels of

endemism among sharks there (Last and Stevens 2009). By contrast, the mid-slope water column around Australia's southeast coast consists of the Antarctic bottom water. This deeper, cooler water has less seasonal variation (than the upper-slope) because the boundary currents are less influential at depth. Most mid-slope sharks have widespread distributions that include more than one oceanic basin. For example *Deania calcea*, occurs in the Atlantic, Indian and Pacific Ocean basins (Moura, Jones *et al.* 2014).

Geomorphology of the Australian continental slope provides some similarities and some contrasts between the upper-slope and mid-slope. The upper-slope seafloor habitat is particularly steep and narrow off most of Australia's south coast, only 2–5 km wide in most places, effectively forming a narrow corridor around the continent with ridges and terraces (AFMA 2012). Similarly the mid-slope seafloor is only 5–10 km in many places (Figure 1.3). Canyons are geomorphic seafloor features on both the upper and mid-slope; Seamounts are more common on the mid-slope (Heap and Harris 2008). These geomorphic features form important habitat that concentrate demersal fish assemblages and the commercial fisheries they support (Pethybridge, Daley *et al*. 2010; Prince 2001).

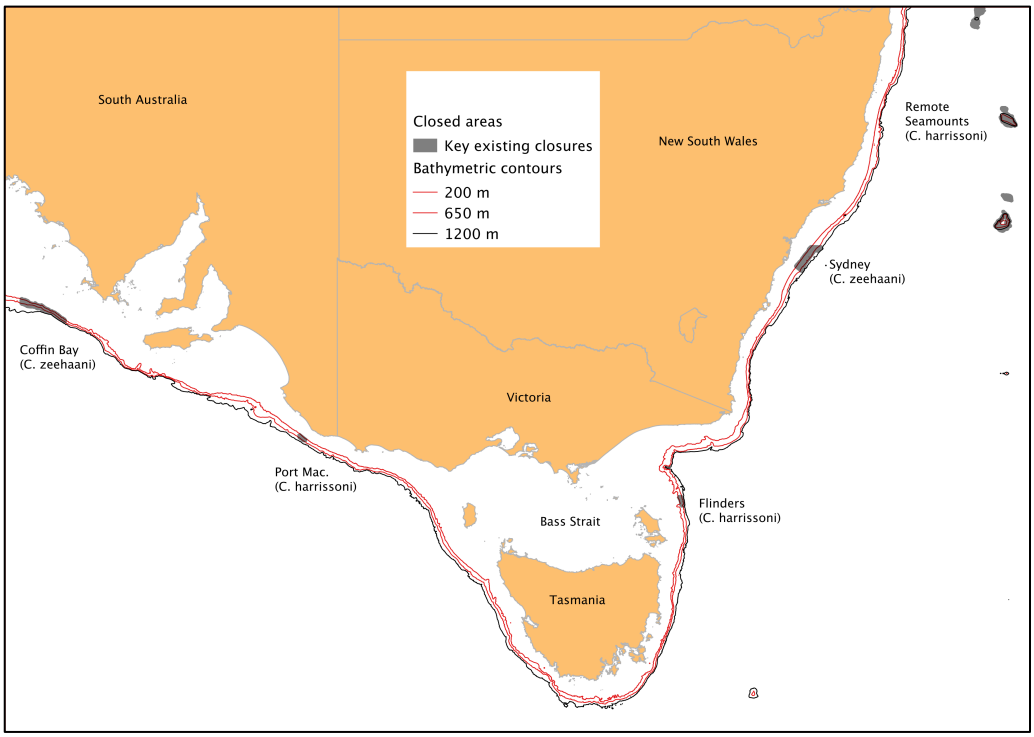


Figure 1.3 Upper-slope and mid-slope demersal bathomes of temperate southeastern Australia showing locations of pre-existing fishery closures for *Centrophorus*.

Trophic ecology and prey movements are potential drivers of movements for predatory sharks. On the Australian upper-slope chondrichthyans species are frequently caught with commercially fished teleosts such as Pink Ling (*Genypterus blacodes*) and Ocean Perch (*Helicolenus barathri*) (Bulman, He *et al.* 2002; Koslow, Bulman *et al.* 1994). Here

dogsharks rely on mesopelagic prey, particularly squids, lantern fishes (Myctophidae), and hatchetfishes (Sternoptychidae) (Pethybridge, Daley *et al.* 2010). Myctophidae dominate in terms of biomass and numbers in continental slope waters and form a key component of the diet of many shark species from both the upper and mid-slope (Daley, Stevens *et al*. 2002; Pethybridge, Butler *et al*. 2012; Williams and Koslow 1997). These mid-water prey species undergo diel vertical migration (DVM) into shallower waters at night, returning to deeper waters during the day. Patterns of diel vertical migration are spatially variable and influenced by variation in physical-chemical properties of water such as oxygen and temperature (Klevjer, Irigoien *et al*. 2016). This process of DVM is an important contributor to the flux of energy between the surface waters, where primary production occurs, and the deep sea (Klevjer, Irigoien *et al*. 2016).

The community structure and trophic ecology of mid-slope waters is well known following studies of the commercial fisheries for Orange Roughy (*Hoplostethus atlanticus*) off Southern Australia and New Zealand. This community is identifiable across a province that extends 5000 km from The Great Australian Bight (Australia) to the Chatham Rise (New Zealand) (Koslow, Bulman *et al.* 1994). Demersal squaliform sharks (mainly Somniosidae and Etmopteridae) dominate the bycatch. These sharks feed on fish and squid and dominate the mid-upper trophic positions (Bulman, He *et al.* 2002; Hallett and Daley 2011). It has been suggested that these shark species could act as top-down predatory regulators of community dynamics (Stevens, Bonfil *et al.* 2000). By contrast Australian upper-slope communities are not well defined.

1.4 Fishery management and conservation

Managing the effects of fishing on Australian deep-sea sharks is complicated by three key factors: 1. species diversity; 2. the range of fishing methods used on different habitats; and 3. multiple jurisdictions (Daley, Stevens *et al.* 2002) (Table 1.2). Early targeted fishing for deep-sea sharks has been halted by catch limits but the effect of bycatch on deep-sea shark numbers remains a problem (AFMA 2012). Early targeted fishing for deep-sea sharks was an unintended consequence of imposing catch limits on commercial bony fish species that resulted in displaced effort that affected that initially targeted deep-sea sharks. Fishing history and independent survey data shows mid-slope sharks were impacted earlier but upper-slope sharks were impacted to a greater extent. (Daley, Stevens *et al.* 2002; Graham and Daley 2011).

The market for liver oil has been the main driver for targeted fishing for deep-sea sharks in Australia and in other countries (Bakes and Nichols 1995; Hernández-Pérez, Gallego *et al.* 1998). In *Centrophorus* and many other species of deep-sea shark, the oil is high in squalene,

a hydrocarbon used in the production of cosmetics and pharmaceutical products with claimed health benefits (Wetherbee and Nichols 2000). In Australia some meat has been marketed, particularly since 2000, but most was discarded, in a wasteful practice referred to as "livering" (Cotton 2010). The Australian liver market supply chain is distinct from the fresh fish market and not well monitored or controlled (Daley, Stevens *et al.* 2002).

Trawl and gillnet vessels have both historically targeted *Centrophorus* spp. on the upper-slope off southern Australia. The combination of methods impacted on *Centrophorus* on both smooth and rough sediments leaving little refuge. Independent trawl survey data showed a decline in catch per unit effort of survey data between 1977 and 1997. This decline has been attributed to the effects of commercial trawling on smooth sediments. (Graham, Andrew *et al.* 2001). *Centrophorus* spp. were also targeted by trawl vessels off eastern Bass Strait and by gillnets set on rough ground around canyon heads off South Australia and eastern Bass Strait. The targeted gillnet fishery was remarkably short-lived in Australia, involving only three vessels. Targeting commenced off South Australia in 1992 and peaked the same year before declining to only 7 t just six years later, when targeting ended (Daley, Stevens *et al.* 2002).

Table 1.2 Australian fisheries that have impacted temperate deep-sea sharks

Jurisdiction	Fishery /sector	Gear	Species	Bathome	Utilisation
AFMA	SESSF/ SET	trawl	*Centrophorus zeehaani, C. moluccensis*	US	L (M), BC
AFMA	SESSF/ SET	trawl	*Deania* spp*, Centroscymnus* spp. *(Etmopterus* spp*)*	MS	L (M), BC
AFMA	SESSF/ GHAT	gillnet	*C. harrissoni, C. zeehaani*	US	L (M)
AFMA	SESSF/ GHAT	auto-longline	*C. zeehaani, C. zeehaani, (Deania spp)*	US	BC
New South Wales	OTLF	bottom line	*Centrophorus squamosus , C. harrissoni, C. moluccensis*	US	L, M
New South Wales	Ocean Trawl	trawl	*C. harrissoni, C. moluccensis*	US	BC
Western Australia/ AFMA	WA gillnet	gillnet	*C. zeehaani*	US	L (M)

AFMA=Australian Fisheries Management Authority; SESSF=Southern and Eastern Scalefish and Shark Fishery; SET=Southeast Trawl; GHAT=Gillnet Hook and Trap; OTLF=Ocean, Trap and Line; US=upper-slope; MS=mid-slope; L=historical targeting for liver, M=historical targeting for meat; BC=bycatch.

Bycatch in trawl continues to be a problem for *Centrophorus* spp. in Australia because these species have low rates of survival when released after capture in nets. The introduction of auto-longline fishing created a new bycatch problem for *Centrophorus* spp. in Australia

(AFMA 2012; Daley, Webb *et al.* 2006). Post capture release survivorship rates for this method are uncertain but between 26–81 % for *Centrophorus* (Williams, Althaus et al. 2013).

Declines in shark catches on the upper-slope in the mid 1990's contributed to a transfer of demand for liver oil to southern Australian mid-slope fisheries. Species of *Deania*, *Centroscymnus* and *Etmopterus* were already common bycatch of the commercially valuable Orange Roughy (*Hoplostethus atlanticus*) fishery around southeastern Australia. From 1992–1995, total allowable catches (TACs) were introduced for Orange Roughy and other commercially valuable bony fishes leading some skippers to target alternative species, including *Deania* and *Centroscymnus* on familiar grounds when TACs were filled (Daley, Stevens *et al.* 2002). Subsequently a collective 'basket' quota was introduced to restrict catches on a group of deep-sea shark species to low bycatch levels. The basket quota was a substantial positive step but catch data are not species specific. Potentially a decline in a more vulnerable species could be obscured among the other basket species (Irvine, Daley *et al.* 2012).

In 2013, *C. harrissoni* and *C. zeehaani* were given national protection in Australia and consequently the major impacting fisheries became responsible for their recovery (AFMA 2012). These species, as well as two other related dogsharks: *C. moluccensis* (Endeavour Dogfish) and *S. chloroculus* (Greeneye Spurdog) are now managed under the Upper-Slope Dogfish Management Strategy (USDMS) administered by the Australian Fisheries Management Authority. The strategy is focused on closures for *C. harrissoni* and *C. zeehaani*, complemented by a zero total allowable catch and code of conduct for the careful handling and release of live sharks caught by line fisheries.

The choice of location for the existing closures for *Centrophorus* was reasonably well founded based on a series of fishing surveys designed for the purpose and undertaken in 2005 and 2009 (Williams, Daley *et al.* 2012) (Figure 1.3). Determining suitable sizes for these closures requires knowledge of the home range and movements of *Centrophorus* (Daley, Stevens *et al.* 2002). Prior to this study there have been no such studies but, assuming larger areas have more suitable habitat, larger is better. All but one of the existing closures extended only 19–56 km along the upper-slope. The much larger closure extends 124 km along the upper-slope, and is located off Coffin Bay (South Australia). This area is a continuous strip of steep upper-slope where *C. zeehaani* were consistently recorded in three surveys from 2005–2009 (Williams, Daley *et al.* 2012). Size, location and abundance of *Centrophorus* made this closure the clear choice for studying home range and movements.

1.5 Home range and movements

Tagging/tracking studies are used to collect movement data for many species including sharks. These data can be used to examine breeding and feeding movements and estimate individual home range (Barnett, Abrantes *et al.* 2010; Heupel and Simpfendorfer 2002). Home range is a key consideration for the design of effective spatial management in fisheries because closures that are smaller than individual home range leave individuals vulnerable to capture when they transit in and out of fished areas (Pecl, Tracey *et al.* 2006).

Tagging/tracking methods can broadly be divided into two types, conventional and electronic. Conventional tagging studies use plastic numbered tags attached to the subject species. A key limitation of the method is that it provides a maximum two observations: release point and recapture point. Conventional tagging methods underestimate movement scale when an individual is recaptured near its release point because the intervening movement is not observed. Passive acoustic monitoring is an emerging electronic tagging method that provides a powerful alternative to conventional tagging for monitoring movements in coastal and continental shelf ecosystems (Heupel, Semmens *et al.* 2006). It involves fitting transmitters to individual sharks and deploying an array of receivers on the seafloor to detect the sharks. Each tagged individual is detected many times, providing statistical power. Tagged individuals do not need to be recaptured, thus reducing stress and additional mortality – a key advantage for vulnerable species.

The earliest example of acoustic tracking of deep-sea sharks was active tracking (from a moving ship) of two individual *Centrophorus acus* on the upper-slope of Suruga Bay, Japan (Yano and Tanaka 1985). One shark swam along the seafloor parallel to the 500 m contour making movements of up to 50 m above the seafloor into the water column; the other died. Recently nine *Centrophorus squamosus* were passively tracked along the mid-slope of the northeast Atlantic (Rodríguez-Cabello, González-Pola *et al.* 2016). This study found two individuals moved more than 1000 km in 80 days and some individuals undertook conspicuous vertical migrations into shallow waters at night.

The analysis of movement data can use top down or bottom up approaches to provide different insights. Top down approaches have been useful for identifying ecologically important variables that influence shark movements, such as day length and temperature; bottom up approaches are generally used for more pragmatic issues such as informing the protection of populations at particular locations (DeAngelis and Grimm 2014; Dudgeon, Lanyon *et al.* 2013). In this thesis, we first applied linear models as a top down approach at the population level to determine if variation in light levels influenced movements. We then

took a bottom up approach using and individual based model (IBM) to model the population response to the modified closure network that was implemented, as well as alternative scenarios. The individual based approach was chosen because individual interactions with environment can lead to emergent properties at the population level (DeAngelis and Grimm 2014).

1.6 Research objectives and thesis structure

This thesis explores conservation and management strategies for deep-sea sharks, focusing on marine spatial management, including closures. The work presents a case study of two upper-slope species that are now protected in Australia and are the subject of a comprehensive management plan that includes closures (AFMA 2012). Three data sets are used: 1. Mitochondrial DNA data (Chapter 2) for identification of species; 2. Passive acoustic telemetry data for examining residency and efficacy of spatial management; 3. Catch data that includes catch, effort, catch value and demographic data (shark size structure and catch ratios) for evaluating closure options against competing conservation and economic objectives.

Chapters 2–5 were prepared as separate scientific manuscripts. Chapter 2 has been published in Marine and Freshwater Research (3 citations) and chapter 3 has been published in Deep-Sea Research II (10 citations). These chapters are presented below in the chronological order they were undertaken and fed-back to managers and industry during the listing process and for developing the recovery plan.

Specifically the research objectives were to:

1. Address taxonomy and identification problems among Australian *Centrophorus* species (Chapter 2, data set 1.).

2. Develop methods for handling deep-sea sharks to ensure survivorship, and collect tracking data (Chapter 3, data set 2.).

3. Develop linear models of residency from telemetry data to determine the efficacy of spatial management for conservation of deep-sea sharks (Chapter 3, data set 2.).

4. Review baseline data on abundance and demographics (size structure and sex ratios) for matching closure location and size to the population distribution (Chapter 4, data set 3).

5. Support development of a coherent spatial management strategy for recovery of deep-sea sharks by clarifying the trade-offs between resource use and conservation in various options (Chapter 4, data set 2, data set 3).

6. Develop timeframes and performance measures to implement the spatial management strategy using simulation modeling (Chapter 5, data set 2).

2

GENETIC CATCH VERIFICATION TO SUPPORT RECOVERY PLANS FOR DEEPSEA GULPER SHARKS (GENUS *Centrophorus,* FAMILY CENTROPHORIDAE) – AN AUSTRALIAN EXAMPLE USING THE 16S GENE

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CHAPTER 2. GENETIC CATCH VERIFICATION TO SUPPORT RECOVERY PLANS FOR DEEPSEA GULPER SHARKS (Genus *Centrophorus,* family Centrophoridae) – an Australian example using the 16S gene

2.0 Abstract

Several species of *Centrophorus* have been harvested beyond sustainable limits in the Pacific, Atlantic, and Indian Oceans. Effective monitoring of current recovery plans in Australia requires the implementation of a catch species data verification plan. The utility of the 16S mitochondrial gene region was evaluated for discriminating among seven recognised morphologically similar *Centrophorus* species caught in commercial fisheries in Australia and Indonesia. The 16S gene amplified consistently, was sequenced in all individuals tested, and was able to distinguish all species with sufficient resolution for routine testing, apart from *C. harrissoni* and *C. isodon*. These two allopatric species were distinguishable using four types of external morphological characters. We conclude that the 16S gene is a robust marker suitable for fishery catch verification of *Centrophorus*, particularly for Australian samples collected under non-ideal conditions for preservation. When combined with morphological characters, this approach is a reliable and efficient system for routine testing. Trials with the CO1 mtDNA gene found that specialised primers are needed; trials with the Cytb mtDNA gene found this marker is sensitive to preservation problems. Future development of the 16S and CO1 markers are likely to contribute to resolution of taxonomic problems within the Centrophoridae.

2.1 Introduction

Centrophorus are medium sized (0.7–1.7 m) demersal sharks from the continental slopes of the world's oceans (Compagno, Dando *et al.* 2005; Last and Stevens 2009). Thirteen species are currently recognised, (Kyne and Simpfendorfer 2010) of which almost half (six species) have been depleted in different areas including the northeast Atlantic, southwest Pacific and Indian oceans (Adam, Merrett *et al.* 1998; Graham, Andrew *et al.* 2001; Heeson 2003; ICES 2010). These include *C. harrissoni* and *C. zeehaani* which are thought to be endemic to southeastern Australia (Last and Stevens 2009; White, Ebert *et al.* 2008) and were recently protected under Australian national environmental law following >90% depletion in some key areas of their historical distribution (Environment 2011; Graham, Andrew *et al.* 2001).

Centrophorus exemplify the highly conserved life histories of deep-sea chondrichthyans with extremely low productivity (Figueiredo, Moura *et al.* 2008; McLaughlin and Morrissey 2005). Australian endemic species such as *C. harrissoni* and *C. zeehaani* have litters of only 1–2 pups (Graham and Daley 2011). Even where trip limits and total allowable catch limits have been implemented to stop targeted fishing in the northeast Atlantic and off south-eastern Australia, these species remain vulnerable as bycatch in multi-species fisheries (Forrest and Walters 2009; ICES 2005). This has led to the implementation of a number of closed areas off southeastern Australia, designed to halt decline and support recovery of *C. harrissoni* and *C. zeehaani* (AFMA 2012). Outside the closures, a code of practice promotes the release of live sharks caught during fishing.

Checking the species composition of *Centrophorus* catches outside the closed areas is important to determine which species continue to be impacted but problematic because *Centrophorus* species are morphologically very similar and the taxonomy of the genus is in need of review (Compagno, Dando *et al.* 2005; Last and Stevens 2009). Mitochondrial DNA (mtDNA) markers have proved useful in species identification of *Centrophorus* and other squaliformes, particularly the cytochrome oxidase 1 (CO1) gene (Moura, Silva *et al.* 2008; Straube, Iglésias *et al.* 2010; Ward, Holmes *et al.* 2008). For other groups of sharks and rays, the 16S rRNA (16S), cytochrome *b* (Cytb) and NADH dehydrogenase subunit 4 (ND4) genes have been used in monitoring trade, in conservation efforts and in catch verification (Chapman, Abercrombie *et al.* 2003; Ovenden, Morgan *et al.* 2010).

In this study, we evaluated the utility of CO1, 16S and Cytb genes in identifying seven *Centrophorus* species. Initially we assessed the efficacy of each gene region in discriminating species based on specimens retained during scientific surveys off Australia and port visits in nearby Indonesia. The 16S marker was then used to verify the identification of tissue samples

taken from16 different specimens caught by commercial fisheries in Australia. The objectives of this study were firstly to support recovery plans for two species of *Centrophorus* in Australia and also to consider the broader utility of the three genes for species level catch verification and taxonomic classification of *Centrophorus* in other regions.

2.2 Materials and methods

Specimen collection and sampling

Whole specimens were collected during scientific fishing operations in Australia and from markets in Indonesia: *C. atromarginatus* (Lombok n = 1), *C. harrissoni* (north-eastern Tasmania, n = 11; Victoria, n=1); *C. isodon* (Bali, n = 3; Lombok, n=1); *C. lusitanicus* (Lombok, n = 1); *C. moluccensis* (Western Australia, n = 3; Bali, n = 2; Lombok, n=1); *C. squamosus* (south-eastern Tasmania, n=2; Java, n = 1); *C. zeehaani* (south-eastern Tasmania, n=2; north-eastern Tasmania, n=1; South Australia, n=3; New South Wales, n=8; Victoria, n=1) (Figure 2.1).

Field species identifications were based on external morphological characters from regional guides from Indonesia (White, Last *et al.* 2006) and Australia (Last and Stevens 2009). Tissue samples (one gram of white muscle) were removed from specimens (whole sharks) and stored in 90% ethanol. Sixteen additional samples (test samples) were collected from Victoria by commercial fishers that had been trained in the use of shark identification guides Specimens were then frozen and shipped with tissue samples to CSIRO, Hobart where identifications were verified at the CSIRO National Fish Collection by international experts including Dr Peter Last, Dr William White and Dr Leonard Compagno. Voucher specimens representing each of the species examined were retained in perpetuity by the Collection (Table 2.1). Preserved tissue samples were also retained by the Collection and stored at –80ºC. Indonesian and Australian specimens of *C. squamosus* were grouped separately and compared because the latitudinal separation between these locations is wider than for any of the other species examined.

DNA extraction, PCR amplification and fragment sequencing

Genomic DNA (gDNA) was extracted using two protocols. For most samples, gDNA was extracted from approximately 25–50 mg of tissue using a modified CTAB (hexadecyltrimethyl ammonium bromide) method (Doyle and Doyle 1987), followed by precipitation with isopropanol and ethanol, and resuspension of gDNA pellets in 100 μl of deionised water. For the test samples, gDNA was extracted using a Wizard SV Genomic DNA Purification Systems (Promega, USA), as per the manufacturer's instructions, using a

final elution volume of 160 μl. Genomic DNA for each individual was quantified using a NanoDrop ND1000 Version 3.0 (NanoDrop Technologies Inc, USA) and diluted to 15 ng/μl, where possible, and stored at 4^0C until used.

Polymerase chain reaction (PCR) amplifications were undertaken using three sets of primers, 16Sar-L and 16Sbr-H (Palumbi, Romano *et al.* 1991), CB1-L and CB2-H (Kocher, Thomas *et al.* 1989) and FishF2 and FishR1 (Ward *et al*. 2005), and used to amplify fragments of the 16S, Cytb and CO1 genes, respectively. Amplification reactions follow protocols for mtDNA haplotype analysis described in (Appleyard, Grewe *et al.* 2001), which provides details of the buffer and polymerase products and volumes used. The reactions were completed in a Perkin Elmer GeneAmp® System 9600 thermal cycler (Applied Biosystems, USA) with annealing temperatures of 54°C for 16S and CO1, and 50°C for Cytb.

PCR products were visualised on 2.5% agarose gels and single banded PCR products for each gene fragment were purified using either Wizard PCR Preps (Promega) (most samples) or AMPure™ magnetic beads (test samples), according to the manufacturers' instructions. We then used 8 –20 ng of purified PCR product (depending on fragment size) as template for bi-directional sequencing using ABI Big Dye® Terminator v. 3.1 Cycle Sequencing kits (Applied Biosystems), using the same primer sets that generated the initial PCR products (listed above).

The resultant BigDye PCR products were then purified either using DyeEx spin columns (Qiagen, most samples) or CleanSEQ® magnetic particles (Agencourt, test samples) according to the manufacturers' instructions. Sequencing was performed on an Applied Biosystems 3130*xl* DNA Autoanalyser following ABI protocols. Reference sequences for the 16S and Cytb gene fragments were submitted to GenBank with accession numbers JN596815-JN596828.

Sequence alignment and data analysis

Sequences from each fragment were edited by eye with Sequencing Analysis v. 5.1 (Applied Biosystems). Fragments were aligned with CLUSTAL X v. 1.81 (Thompson, Gibson *et al.* 1997) using default parameters. The aligned sequences were analysed in MEGA v3.1 (Kumar, Tamura *et al.* 2004). Neighbour-joining (NJ) trees (Saitou and Nei 1987) based on Kimura 2-parameter (K2P) distances (Kimura 1980) were produced with the pairwise-deletion option selected. The NJ trees provide a graphical representation of the pattern of divergence among the *Centrophorus* individuals and species. *Squalus acanthias* (GenBank

Accession Number Y18134) was used as the outgroup for tree analyses. Reliability of the resulting clades was estimated using 1000 bootstrap replicates (Felsenstein 1985).

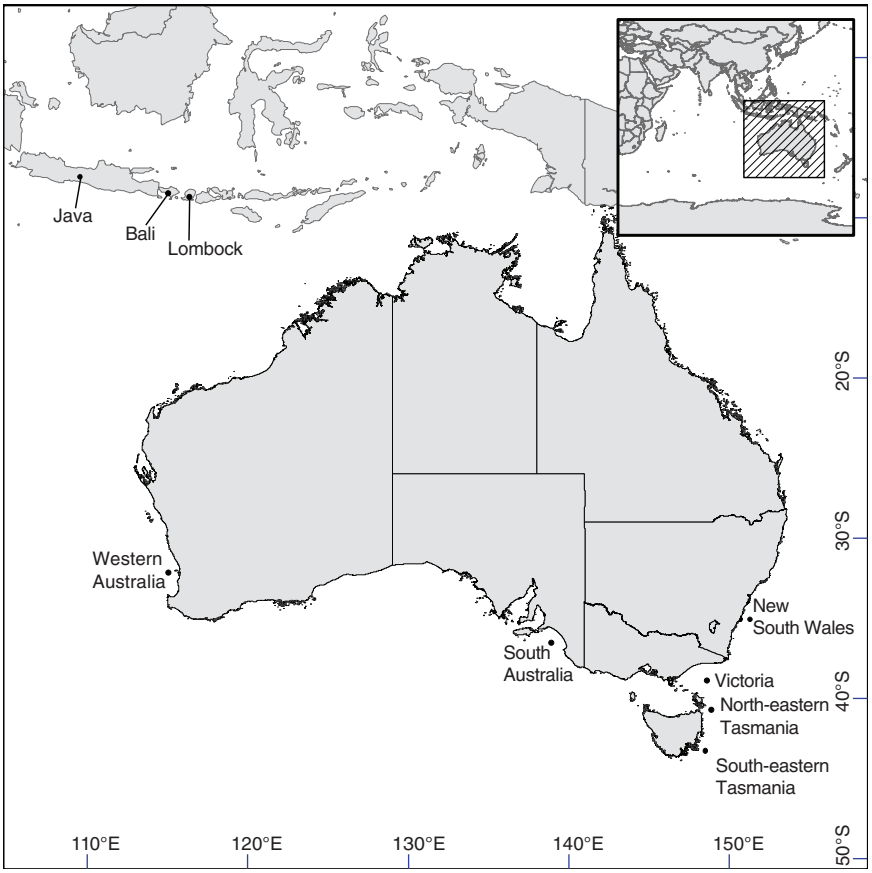

Figure 2.1 Capture locations in the Indo-west Pacific for *Centrophorus* spp. examined using 16S mtDNA fragment.

Genetic diversity indices were estimated for three Australian species that are taken as fishery bycatch and had at least five samples available: *C. moluccensis, C. harrissoni,* and *C. zeehaani.* Genetic diversity indices were estimated in ARLEQUIN version 3.1 (Excoffier, Laval *et al.* 2006) and included the number of haplotypes, number of variable positions, and nucleotide diversity (π).

Table 2.1 Representative voucher specimens available at the CSIRO National Fish Collection for *Centrophorus* species collected from Australia (A) and Indonesia (I).
Locations denoted [m] were market locations approximating the capture locations.

Species	Group	Region	Location	CSIRO Voucher No.
C. zeehaani	1	Australia	Victoria	H 6503-03
C. moluccensis	2	Australia	Western Australia	H 3599-04
C. moluccensis	2	Indonesia	Bali [m]	H 5857-03
C. atromarginatus	3	Indonesia	Lombok [m]	H 5788-01
C. squamosus [A]	4	Australia	south-eastern Tasmania	H 4873-03
C. squamosus [I]	4	Indonesia	Java [m]	H 5860-09
C. lusitanicus	5	Indonesia	Lombok [m]	H 5788-02
C. harrissoni	6	Australia	north-eastern Tasmania	H 6500-03
C. isodon	6	Indonesia	Lombok [m]	H 5875-04

2.3 Results and discussion

Sequence variation

Only the 16S gene was consistently amplified and sequenced in all samples in this study, including the test samples. Previous studies using the 16S also found the marker to be robust for catch species verification of sharks, even for dried fins (Woodley, Chapman *et al.* 1994). In contrast, amplification and sequencing of the Cytb gene was problematic for samples collected from Indonesian markets in particular where some DNA degradation is likely to have occurred. Sharks that are caught and sold commercially will never be stored under ideal conditions for tissue preservation, therefore the Cytb gene was not considered sufficiently robust for routine catch species verification.

When the CO1 gene was trialed using the conventional degenerate primers, multiple bands were observed on the agarose gels, indicative of multiple PCR products. Previous trials of CO1 gene in *Centrophorus* (Ivanova, Zemlak *et al.* 2007; Ward, Zemlak *et al.* 2005) were more successful, but only when pair-wise combinations of CO1 primers and M13-tailed primer cocktails were used. These results indicate the CO1 gene has potential application to genetic taxonomy and classification but for routine catch species verification, this additional complexity would be cumbersome. Therefore the remainder of this paper will focus exclusively on the data obtained from the 16S fragment.

All sequences obtained were visually checked using chromatogram outputs from Sequencing Analysis v. 5.1 (Applied Biosystems). The start and end of each sequence was edited with particular care to eliminate primer information and any nucleotides that could not be identified unequivocally. The edited fragment lengths did not vary significantly between species ranging from an average of 486 base pairs (bp) in *C. harrissoni* to 505 bp in *C. zeehaani*. When the 42 individuals (excluding the test samples and the outgroup) were

checked using bi-directional sequencing, the nucleotides identified in the forward sequence were identical to the reverse sequence for, on average, 499 nucleotide pairs. Where the forward and reverse sequences did not match, transitional pairs (n = 4) outnumbered transversional pairs (n = 1). Average nucleotide frequencies across the 58 individuals were T = 28.4%, C = 20.5%, A = 32.0%, G = 19.1%.

The 16S gene region showed more between than within species variation, The NJ tree separated the *Centrophorus* species from the outgroup and provided some separation between the six groups. Average K2P distance among the individuals within species was 0.010 (± 0.003) (in-groups only excluding the test samples). Genetic distances were as low as 0.001 between some species but, importantly, were .005 or greater for the main species caught by Australian fisheries (*C. harrissoni*, *C. moluccensis* and *C. zeehaani*) (Table 2.2). This indicates the 16S marker is suitable for routine catch species verification in Australia.

Table 2.2 Summary of K2P genetic distances based on the 16S gene fragment sequenced among the *Centrophorus* from Australia (A) and Indonesia (I).
Distances below diagonal; standard errors above diagonal. Australian and Indonesian specimens of *C. squamosus* designated A and I. Excludes test samples.

Species	C. z	C. s ^{A}	C. s ^{I}	C. h	C. i	C. l	C. m	C. a
C. zeehaani	-----	0.005	0.005	0.005	0.005	0.004	0.005	0.004
C. squamosus ^{A}	0.013	-----	0.001	0.005	0.005	0.003	0.006	0.005
C. squamosus ^{I}	0.012	0.001	-----	0.004	0.001	0.003	0.006	0.005
C. harrissoni	0.014	0.011	0.010	-----	0.001	0.003	0.006	0.005
C. isodon	0.015	0.011	0.011	0.001	-----	0.004	0.006	0.005
C. lusitanicus	0.008	0.005	0.004	0.006	0.007	-----	0.005	0.004
C. moluccensis	0.014	0.017	0.016	0.018	0.019	0.012	-----	0.004
C. atromarginatus	0.010	0.013	0.012	0.014	0.015	0.008	0.008	-----

Following inclusion of the test samples, the NJ tree separated the individuals into six putative species groups: 1. *C. zeehaani*, 2. *C. moluccensis*, 3 *C. atromarginatus*, 4. *C. squamosus* north/*C. squamosus* south, 5. *C. lusitanicus*, 6 *C. harrissoni*/*C. isodon*. The largest division was between *C. zeehaani,* considered to be an Australian endemic (White, Ebert *et al.* 2008), and the remaining *Centrophorus* spp. Small divisions separated all currently recognised species apart from *C. harrissoni*/*C. isodon* indicating the 16S gene has the potential to contribute to future genetic classification studies of *Centrophorus*. Exploring this potential will require larger samples sizes for some species, particularly for *C. atromarginatus* and *C. lusitanicus* represented by only one sample in this study. The published distributions of these species are patchy and uncertain therefore it will be difficult to collect geographically representative tissue collections from limited sampling opportunities (Compagno, Dando *et al.* 2005)

The lack of genetic separation between north and south samples of *C. squamosus* supports the laboratory identifications of the two vouchers as the same species. This indicates some level of mixing between Indonesia and south-eastern Tasmania, even though these sites are widely separated. The lack of separation between *C. harrissoni* and *C. isodon* was an unexpected pattern because these recognised species are separable using fin colour, morphometrics, denticle shape and tooth shape (Compagno, Dando *et al.* 2005; White, Ebert *et al.* 2008). This suggests some limitations on the overall utility of the 16S marker. However, this should not be problematic for catch species verification in Australia because the species are allopatric: *C. harrissoni* occurs off eastern Australia and remotes seamounts in the Tasman Sea, whereas *C. isodon* is restricted to the north Indian Ocean and the northwest Pacific Ocean. The 16S marker has been more successful in studies of the carcharhiniform sharks, although the fragment examined was much longer, up to 1452 bp (Iglésias, Lecointre *et al.* 2005; Woodley, Chapman *et al.* 1994).

16S Sequence variation within Centrophorus taken by Australian fisheries

The nucleotide sequences of the 16S gene region obtained for specimens of Australian *C. harrissoni, C. moluccensis* and *C. zeehaani* matched their field identifications. Nucleotide variation was low, comparable with previously published studies of mitochondrial genes in sharks (Table 2.3) (Moura, Silva *et al.* 2008; Ovenden, Morgan *et al.* 2010; Veríssimo, McDowell *et al.* 2010; Veríssimo, McDowell *et al.* 2011; Ward, Holmes *et al.* 2008). The number of haplotypes was low ranging from three in *C. moluccensis* to six in *C. harrissoni* and *C. zeehaani*. Only two or three nucleotide sites were variable in these species. Within species, genetic variation was highest in *C. harrissoni* ($\pi = 0.071$) and lowest in *C. moluccensis* ($\pi = 0.001$).

Some of the test samples of *C. harrissoni* and *C. zeehaani* show small levels of separation from samples of the same species collected from scientific surveys (Figure 2.2). This is attributed to individual variation, rather than geographic separation because the test samples and survey samples of both these species include samples from Victoria. The test samples of *C. moluccensis* show a larger separation from the survey samples and market samples. It is possible that this represents geographic separation because the test samples were collected from Victoria whereas the other samples were collected from Western Australia and Indonesia. This would be consistent with previous suggestions that *C. moluccensis* could represent more than one species (Compagno, Dando *et al.* 2005).

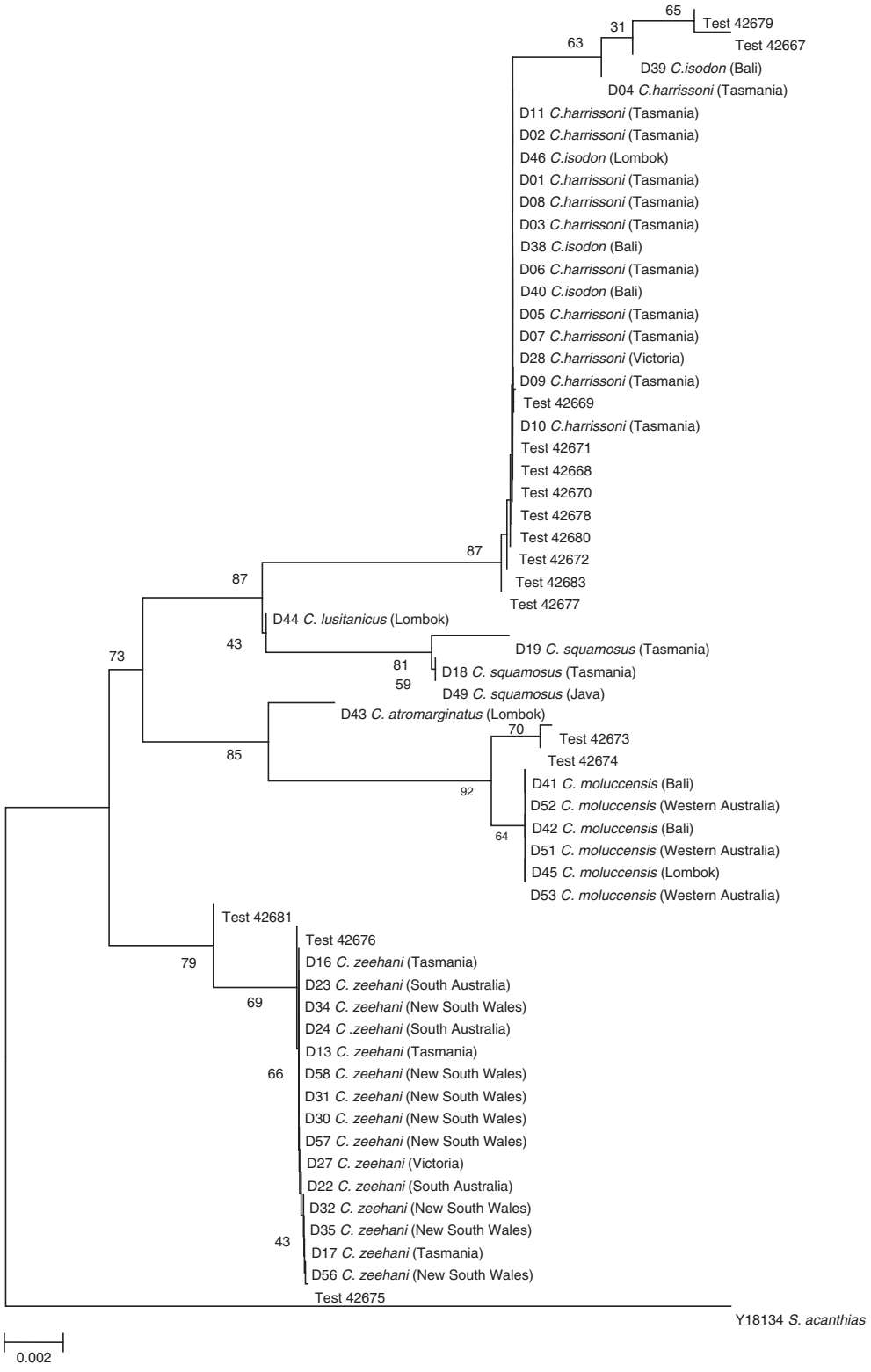

Figure 2.2 16S mtDNA phenogram for western Pacific *Centrophorus* species. Produced in MEGA using K2P distance and NJ tree algorithm (robustness of tree topology calculated after 1000 bootstrap replications). Commercial samples are prefixed by D426. TAS=Tasmania, NSW=New South Wales, WA= Western Australia, SA= South Australia.

Table 2.3 Summary of the polymorphism statistics for the 16S rRNA fragment for *C. harrissoni, C, moluccensis, C. zeehaani* individuals from Australian waters.

Group	Sample size	Average length (bp)	Number of haplotypes	Variable sites	$\pi \pm SD^a$
C. harrissoni	23	486	6	2	0.071 (0.040)
C. moluccensis	5	503	3	2	0.001 (0.001)
C. zeehaani	18	505	6	3	0.004 (0.002)

a π = nucleotide diversity/average gene diversity over all loci assuming two randomly chosen homologous nucleotide sites are different. bp=base pair.

A number of species of *Centrophorus* and related species from the family Squalidae are mainly restricted to the upper-continental slope bathome, that is the seafloor between the 200 and 650 m depth contours (Last and Stevens 2009). This habitat is particularly steep and forms a narrow ribbon-shaped strip of habitat only two miles wide in many places leading to high levels of endemism (Last and Stevens 2009; Williams, Barker *et al.* 2005). Consequently even localised impacts on upper-slope shark populations are likely to fragment habitats and species distributions leading to reduced genetic diversity. A loss of genetic diversity can reduce overall species fitness due to genetic drift leading to negative consequences such as lowered resistance to disease or ability to adapt to climate change. Genetic examination of population structure will be therefore be key to understanding the likelihood that depleted species can recover from fishery impacts. Currently there are only limited genetic markers available for *Centrophorus* in particular and there is an immediate need for additional development.

Conclusions

The 16S marker distinguished all Australian *Centrophorus* spp. using universal primers, even when samples were not in ideal condition. This marker is suitable for implementation of an ongoing catch species verification program in Australia, which is essential to monitor species recovery, and has potential for use in catch species verification in other regions including Indonesia. Further marker development is needed for species identification in *Centrophorus,* including 16S and CO1. Marker development is also needed to address conservation risks due to unknown stock structure. This research is the first to apply the 16S genetic marker in *Centrophorus* and increases the range of sequence information now available for the group.

3

CAN MARINE RESERVES CONSERVE VULNERABLE SHARKS IN THE DEEP SEA? A case study of *Centrophorus zeehaani*, (Centrophoridae) examined with acoustic telemetry

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CHAPTER 3. CAN MARINE RESERVES CONSERVE VULNERABLE SHARKS IN THE DEEP SEA? A case study of *Centrophorus zeehaani,* (Centrophoridae) examined with acoustic telemetry

3.0 Abstract

Centrophorus zeehaani is one of at least 10 deep-sea shark species globally suffering major population declines attributable to expanding human resource use. Spatial closures have the potential to contribute to recovery of populations if home range and movements can be studied and understood. We implemented the first passive acoustic tracking study of sharks in the deep ocean (300–700 m depths) to evaluate the effectiveness of a large (˜120 km long) fishery closure off southern Australia implemented to protect *C. zeehaani.* Using an array of 21 moored acoustic receivers, we passively tracked 71 tagged individuals over a 15 month period. Sixty-one sharks were detected repeatedly over an average duration of 408 ± 153 days. The average along-slope range was 19.2 ± 12.2 km and the maximum was 75 km – the full width of the array. Each month an average of 0.71 fewer males were detected; the number of females detected did not vary significantly between months. Individual males left the closure, but returned during the study period. Movement along-slope was influenced by month and release point, with shifts south and eastward occurring during austral winter — particularly by some males. Detection depth was strongly correlated with seafloor depth confirming that synchronous diel vertical migration (night time ascent) between population average depths of 640 m and 340 m occurred mainly on the seafloor. Different individuals occupied different depths on the seafloor. We conclude that the closure studied is effectively located to help conserve *C. zeehaani* because it has sufficient along-slope extent and depth range to encompass the home range of a high proportion of the individuals in the local population. Our work demonstrates the utility and uncertainties associated with acoustic tracking in the deep ocean, and the need to evaluate species movement and behaviour when relying on spatial closures to meet conservation objectives.

3.1 Introduction

Centrophorus are medium sized (0.7–1.7 m) demersal sharks widely distributed in the world's oceans (Compagno, Dando *et al.* 2005; Kyne and Simpfendorfer 2010; Last and Stevens 2009). They are particularly well adapted to the stable environment of the deep sea, exemplifying the typical attributes of K-strategists such as long generation time and few offspring (Figueiredo, Moura *et al.* 2008; McLaughlin and Morrissey 2005). Some *Centrophorus* species have only 1–2 pups per litter, although the gestation period is uncertain (Graham and Daley 2011). As a consequence, *C. zeehaani* populations are likely to take decades or centuries to recover following over-exploitation (Kyne and Simpfendorfer 2010).

Six *Centrophorus* species have been depleted in the northeast Atlantic, southwest Pacific and Indian oceans (Adam, Merrett *et al.* 1998; Graham, Andrew *et al.* 2001; ICES 2010). Targeted fishing has largely extirpated *C. harrissoni* and *C. zeehaani* from parts of their range, particularly off southern New South Wales (Graham and Daley 2011; White and Kyne 2010), leading to national-scale protection in Australia in 2013 (Environment 2013). Although measures have been introduced to end targeted fishing for *Centrophorus* in the northeast Atlantic and off south-eastern Australia, these species remain vulnerable as bycatch in multi-species fisheries (Forrest and Walters 2009; ICES 2005). Strategies that include area closures to all methods of fishing are likely to represent the only effective solution for such species (Daley, Appleyard *et al.* 2012; Forrest and Walters 2009) (Chapter 2).

Spatial closures are a key strategy for managing fishing and other human activities that impact biodiversity (Sobel 1993; Sumaila, Guénette *et al.* 2000). The overall efficacy of the approach in the deep sea is difficult to predict because the environment is poorly understood compared to continental shelf ecosystems. Location and size are key design considerations for understanding the inevitable trade-offs between resource use and conservation associated with the implementation of fishery closures and other forms of spatial management (Chittaro, Kaplan *et al.* 2010; Ruijs and Janmaat 2005). Closures are likely to be effective for shark species that have individual home ranges of intermediate scales: tens of km wide (Bonfil 1999).

At least seven species of *Centrophorus* are recorded from Australian waters (Last and Stevens 2009; White and Kyne 2010). This paper focuses on a species still formally recognised as *Centrophorus zeehaani* from southeastern Australia. A recent genetic study found it to be genetically identical to specimens collected from the eastern Atlantic (Naylor, Caira *et al.* 2012) and *C. zeehaani* is likely to be synonymized with another species with nomenclature to be determined (William White, CSIRO National Fish Collection, personal communication).

In Australia at least, distribution is restricted to temperate waters of the upper-continental slope within a narrow bathymetric range from 250–800 m (Duffy 2007; White, Ebert *et al.* 2008; Williams, Althaus *et al.* 2013). Here this ecologically distinct 'bathome' (Last, Lyne *et al.* 2010) is particularly steep, forming a narrow corridor of habitat, < 5 km wide in many places making it particularly vulnerable to fragmentation by localised fishery impacts.

A network of closed areas and other complementary measures have been developed for *Centrophorus* by State and Commonwealth fisheries management agencies off southeastern Australia. Protective closed areas have been implemented by the Australian Fisheries Management Authority with the support of the fishing industry, specifically to 'halt declines' and 'support the recovery' of *C. harrissoni* and *C. zeehaani* (AFMA 2012; Daley, Appleyard *et al.* 2012) (Chapter 2). These provide an opportunity to examine the data needs and logistical and technical challenges associated with their design and subsequent monitoring. The largest and longest established of these closures is for *C. zeehaani* off southern Australia. Its design was based on fisher's knowledge of a location where male and female *C. zeehaani* occur together across a strip of steep upper-slope about 50 km in length, but only 3–5 km wide. The presence of mature breeding females at this location was considered important to the breeding success of the population. Fifteen km wide buffers were added to the eastern and western margins of the area identified by fishers to mitigate edge effects. Edge effects can occur if sharks resident near the edges of the closure move in and out periodically interact with legal fishing just outside the residence area. Reliable data is needed to determine if the scale of these closures is adequate to encompass the scale of home range, which has not previously been measured for any *Centrophorus* species.

Passive acoustic telemetry is now an established method for examining the home range and essential habitat in the context of the design of closed areas for management purposes (Andrews and Quinn 2012; Heupel, Semmens *et al.* 2006). The method involves fitting acoustic transmitter tags to individual sharks and deploying an array of receivers to detect tagged sharks in proximity to the receivers (Heupel, Simpfendorfer *et al.* 2004; Knip, Heupel *et al.* 2012). Passive telemetry has some key cost and logistical advantages over conventional tagging for deep-sea observation. Data are compiled remotely such that the instruments only need to be accessed every 6–12 months. There have been no previous attempts at passive acoustic telemetry in the deep sea to date and only a few studies have used active telemetry tracking, e.g. Yano and Tanaka (1986) actively tracked the movements of a single *Centrophorus acus* along the 400-m contour in Suruga Bay, Japan.

Here we describe the first comprehensive passive acoustic telemetry study of sharks on the continental slope. We consider the efficacy of the largest of the spatial closures implemented for *C. zeehaani* using summary metrics of duration, linear distance and a residency index to determine the extent that *C. zeehaani* stay within the closure area. Two models are developed to describe movement along-slope (longitude) and across-slope (seafloor depth). The results are discussed in relation to managing a broader range of deep-sea shark species, and the associated research needs.

3.2 Materials and methods

The study site is located within a fishery closure approximately 100 km long and 8–12 km wide implemented for *C. zeehaani* in temperate waters of the upper-continental slope c. 190 km southwest of Coffin Bay, southern Australia (Figure 3.1). The seabed within the closure comprises c. 250 km^2 of predominantly muddy terraces interspersed with many small canyons and intervening ridges and scattered patches of outcropping rock and small rocky hills.

Acoustic receiver array

Passive acoustic monitoring of tagged *Centrophorus* at the study site was undertaken using an array of 21 Vemco VR2 acoustic receivers (Vemco Ltd., 2013) arranged in curtains. Each curtain consisted of a group of 3–4 receivers in a line. A series of five curtains of receivers were positioned along the upper-slope 17–21 km apart to examine seasonal variation in along slope distribution of the population: Far East, East, Central, West and Far West (Figure 3.1). The West, Central and East curtains span the core of the closed area corresponding to the area where fishery data showed male and female *C. zeehaani* were present. The outer Far West and Far East curtains are within the buffer zones added to the closed areas to manage edge effects. Detection range was measured at the site using a towed transmitter and found to extend to a maximum radius of 900 m, with 95% of transmissions detected within a radius of 650 m (Williams, Daley *et al.* 2012).

Survey data indicate *C. zeehaani* on the east coast of Australia move shoreward into shallow waters at night and move offshore to deeper waters during the day (Williams, Althaus *et al.* 2013). Our receiver curtains were configured to test for similar patterns off southern Australia. Within each curtain, receivers were positioned approximately 1000 m apart (so the detection radii of adjoining receivers overlapped) in lines up to 5 km long. Closer spacing was used near hills to avoid shadowing. Curtains spanned the width of the upper-slope in depths from 225–660 m (Figure 3.1). Two additional receivers were deployed separately as isolated "listening stations" on a ridge and near a canyon (Figure 3.1) to examine the effects of seafloor habitat type on distribution of the population along the slope.

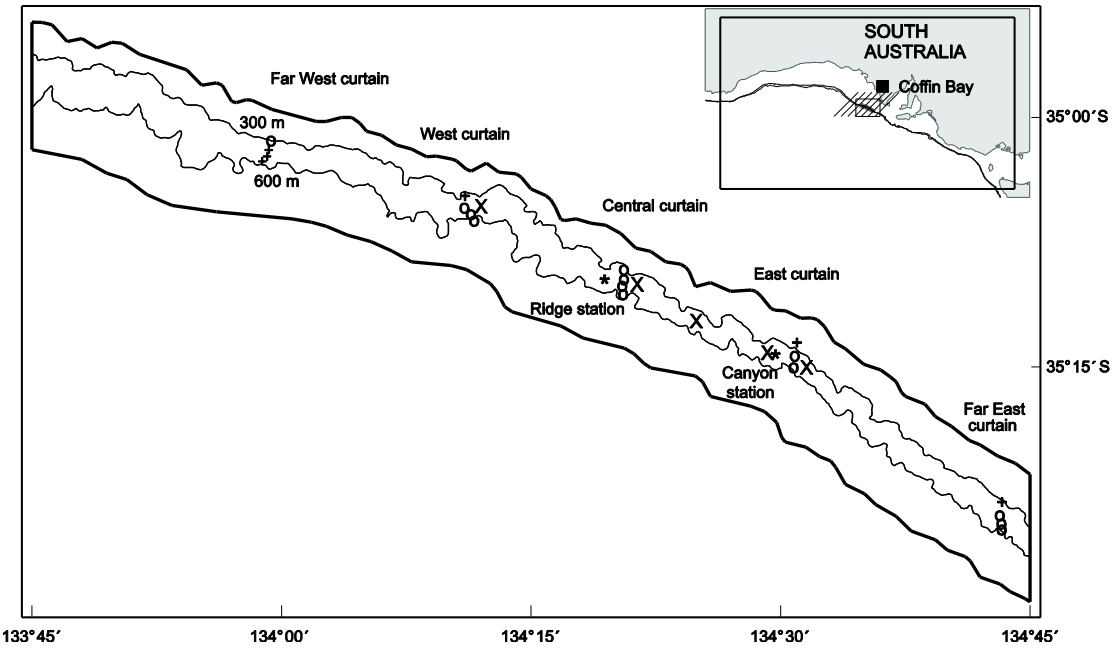


Figure 3. 1 (and inset) Location map of the study site and configuration of the acoustic receiver array used for passive acoustic telemetry study of *Centrophorus zeehaani* on the upper continental slope off southern Australia.
(o) recovered curtain mooring; (+) missing curtain mooring; (*) recovered station mooring; (X) tag and release location; heavy line indicates closure boundary; light line indicates 300 m and 600 m bathymetric contours.

Receivers were moored separately, 100 m above the seafloor. Each mooring consisted of 100 m of polypropylene rope with high-pressure floats (total 35 kg buoyancy) at the top. Receivers were attached just below the floats using a custom nylon bracket (Williams et al., 2012). The base of each mooring line was attached to a 250-kg weight using a Coastal Acoustic Release Mechanism (CART) (Underwater Video Systems, 2012). A 35-m fishing vessel was used to deploy the moorings. Moorings were initially deployed on 10 November 2008, recovered and redeployed after one year to replace the batteries, and finally recovered on 1–2 November 2010. Moorings were released by activating release mechanisms using a hydrophone lowered over the side of the vessel. The receivers were then recovered once they had floated free to the surface. Data were downloaded from recovered receivers during the battery change and at the end of the study period.

Tagging, survivorship and data quality

Sharks were captured in August 2009 using longlines set along the seafloor prior to dawn in the core of the study area. Each line had 1,500 hooks (size 12/0) attached to 0.4-m snoods (1.8-mm monofilament) that were tied at 0.7-m intervals to the mainline (7-mm diameter). Sixty-kg weights were attached to each end and the line was laid out under tension. Extra weights and floats were clipped to the mainline to prevent drifting or snagging depending on

the sea-floor terrain. Hooks were baited with either Australian sardine (*Sardinops neopilchardus*) or Gould's squid (*Nototodarus gouldi*). Fishing was undertaken during cool winter nights to minimise temperature stress to the sharks upon bringing them to the surface and limited to a three hour set time to reduce struggling on the line.

Acoustic tags (Vemco V16: 69 kHz, 60–180 second interval, 4H battery, estimated tag life ~ 2 years) with depth and temperature sensors were attached to the dorsal fin of adult *C. zeehaani* using two 4-mm steel bolts secured with 'Nyloc' nuts and a backing plate. Maturity was determined by clasper calcification for males and total length of females (Graham and Daley 2011). Tagged sharks were released at the surface immediately after tagging at the capture locations to minimise stress.

Two preliminary checks were made to ensure data quality. Firstly any single detection by a given shark within a 60 minute period was considered potentially spurious (false detection) and excluded from analysis, as recommended by the receiver manufacturer (VEMCO personal comm.). To check all sharks had returned to normal behaviour quickly following capture, the depth and longitude data for the first week following release were plotted separately for each individual and checked for static data (dead), or rapid dives or ascents (stressed).

Residency

Four metrics (modified from (Bond, Babcock *et al.* 2012) were used to summarize residency results for individual sharks. The summary metric data consisted of one measurement per shark for each of the summary metrics: Number of Days detected (N days) is the count of calendar days detected. Duration (DUR) was measured as the period between shark release date and the last date detected. Maximum Linear Distance (MLD) was measured as the linear distance (displacement) between the western most and eastern most receivers where an individual was detected. Daily detection Index (DI) was the number of days detected/days at liberty and was expressed as a fraction. The effects of sex and release curtain (categorical variables) on the summary metrics were tested using Analysis Of Variance (ANOVA). Although only large mature sharks were used in the study, any residual effects of length on the summary metrics were tested for significance using linear regression.

Residency was also examined using monthly filtered data: a sub-set of the detection data obtained by selecting the first detection per individual per month. These data were used to determine monthly counts of males and females detected. Linear regression was then applied to these counts to determine if non-resident individuals were leaving the closure area during

the study. Females and males were treated separately. All statistical analyses were completed in the R statistical computing environment (R Core Development Team 2012).

Movement along-slope (longitude)

A Generalized Additive linear Mixed-effects Model framework (GAMM) was used to describe displacement along-slope (east-west) from points where sharks were released, as a measure of home range. The model was developed using daily filtered data: a sub-set of the detection data obtained by selecting the first detection per individual, per day. It was assumed that distributional shifts along-slope occurred over longer timescales in response to seasonal or monthly cycles. The along-slope GAMM model develops a smooth function of the detection location relative to the release location to describe east-west response. Candidate models are evaluated primarily by comparing the smooth function to dependent variables with similar frequencies. The primary dependent variables were calendar month and moon cycle. These were treated as cyclic variables, because they always return periodically to the initial state. Moon illumination data were obtained from the R statistical Package 'phenology' (Girondot 2013) and expressed as % cycle towards next full moon. Release longitude was obtained from the tagging data and treated as a non-cyclic variable.

Seafloor habitat type (ridge, canyon or terrace) at the release point was determined from detailed bathymetric data acquired and processed at sea during the initial phase of the field program (Williams, Daley *et al.* 2012) and incorporated as a categorical variable. Sex was not included due to the unbalanced number of males (58) and females (13). The analyses used a Gaussian error structure with an identity function to link the observed data to the predicted error structure. Tag number was treated as a random factor to allow for individual variation in the model and enable model predictions to extend to the rest of the population (Venables and Dichmont 2004). GAMM model frameworks were implemented using the GAMM4 packages in R and optimised to minimise the Akaike Information Criteria (AIC). The AIC is a measure of the relative quality of a statistical model that deals with the trade-off between goodness of fit and complexity. The random effects due to individual sharks were reviewed by plotting the density of the multiple random errors as a proportion of the number of detections in the daily filtered data.

Across-slope (depth related) movement

A second GAMM framework was used to describe diel variation in depth. It was assumed that depth responses would include daily variation; therefore the model was based on hourly filtered data: a sub-set of the detection data obtained by selecting the first detection per individual, per hour. The across-slope GAMM develops a smooth function of the depth

sensor data to determine that the response is influenced by daily or other variables. Cyclic hour of the day was used as the leading variable in each candidate model for depth. A change in depth can potentially reflect a change in position in the water column, movements along the seafloor across bathymetric contours, or a combination of both. If movement is mainly along the seafloor then the depth data transmitted by the pressure sensors on tagged *C. zeehaani* should be highly correlated with the seafloor depths at the receivers. Correlation was tested using linear regression and it was expected that a linear function with a slope of close to 1.00 and a y-intercept of zero would indicate average depth was near the seafloor.

3.3 Results

Acoustic receiver array

Fifteen of the 21 receivers were recovered at the conclusion of the study period; receivers were lost at four of the five curtains: Far West (3/4), West (1/4), East (1/3), Far East (1/4) (Figure 3.1). Localised paired abrasions, consistent with sharks dentition, of some recovered mooring lines suggests that shark bite might have been responsible for some of the losses. Corrosion of the release mechanism also appears to have led to mooring losses because some release mechanisms were detected by the acoustic control hydrophone, which emitted the release code, but failed to activate the release.

Tagging and survivorship

Acoustic tags were fitted to 13 females (F) and 58 males (M) released in the core of the study area: West curtain (7F, 8M); Central curtain (1F, 5M); midway between Central curtain and East curtain (1M); East curtain (3F, 35M); canyon near East curtain (2F, 9M). Release depth was generally within the range of 320–520 m, except at the West curtain where the release depths ranged more widely from 270–635 m. Tagged sharks had total lengths of 91–112 cm (females) and 85–102 cm (males) and all the males had fully calcified claspers. Full details of the tagged sharks are given in Appendix I. The downloaded data included 59 *C. zeehaani* that were detected on at least three calendar days and by at least two receivers. Nine sharks were never detected after the release day.

The depth data were used to check survivorship. Two *C. zeehaani* initially showed variation in depth but later the depth became static (more than 100 sequential detections at the same depth). This indicates that the sharks died near receivers during the experiment. Static depth data were excluded from analysis. Tag shedding is unlikely because the acoustic tags were double steel bolted to the first dorsal fin.

Residency

Examination of the summary metrics showed that on average, individuals detected after the release date continued to be detected during most of the study, if infrequently (Supplementary Table B). The number of days detected varied widely from 1–294 ($\bar{x}$ = 78 ± 9.6, Supplementary Tables A and B). Similarly Duration varied widely from 6–488 days but mean DUR was high: $\bar{x}$ = 408 ± 19. Mean DI was 17% ± 2%; lower than expected given the high mean DUR.

Mean individual MLD was 19.9 ± 2.6 km. This represents less than half the width of the closure. The range of MLD values was wide: 2–75 km, indicating high individual variation. Six individuals had MLD of < 10 km, indicating they were only detected at two adjacent receivers in one curtain. Sixteen individuals including three females, moved across > 52 km representing the distance across four curtains, and one of these, a male released at the East curtain, was detected across 75 km representing the linear distance across all five curtains in the array.

When the variance in individual DUR, DI and MLD were examined for the effects of gender, release curtain and habitat, no significant differences were found (Supplementary Table B). Shark length was significantly and positively correlated with N days, even though only large adults were used (P = 0.0345). Overall these results indicate individual variation in movement patterns is a key factor contributing to the wide range of values in the other summary metrics.

As the DI was low, residency was analysed on a monthly scale. Linear regression showed that the number of males detected within the array declined significantly (P < 0.001) by an average of 0.71 males per month (Figure 3.2). By contrast, there was no evidence of a decline in the number of female sharks detected over time (P = 0.153).

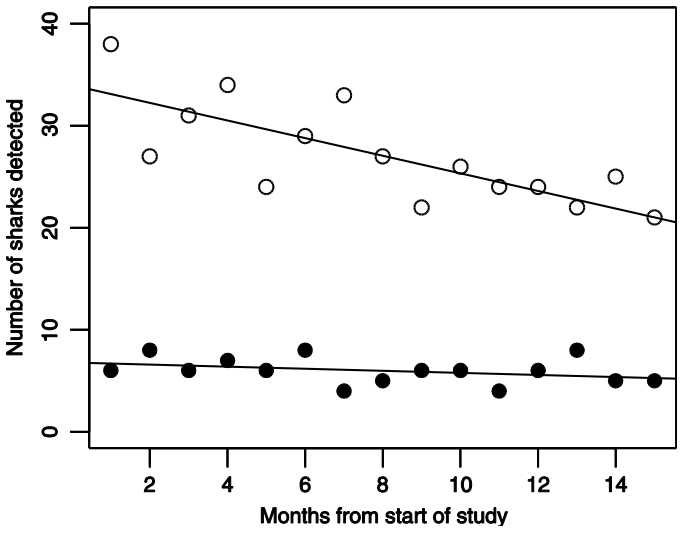


Figure 3.2 *Centrophorus zeehaani* detected from a pool of 58 tagged males (open circles) and 13 tagged females (closed circles) within the receiver array off southern Australia over a 15-month period. (Note 9 tagged sharks were never detected.)

Movement along-slope (longitude)

The daily filter selected 6053 unique combinations of tag and day from > 100,000 detections. A series of seven candidate models were developed (Table 3.1). Two candidate models without tag included as a random factor performed poorly (ΔAIC > 7200). Three candidates that combined the 3 factors of release longitude, month, and random tag fitted the data similarly well (ΔAIC $\leq$ 5). Adding habitat as a fourth factor appeared to improve the model slightly but adding length did not.

The candidate with the lowest AIC was chosen as the preferred model (top of Table 3.1, Table 3.2). This included smoothed functions of release position and month, with habitat added and tag included as a random factor. The intercept and overall average displacement was - 6.81 ± 4.10 km (west) of the release point, which was not significantly different from zero (release point) (P = 0.097). This indicates the average daily location of most individuals during the study was near their release location. Release habitat was not influential (P > 0.8).

When the smooth terms were considered, both release longitude and month were significant (P < 0.001) (Table 3.2). Release longitude had 1.000 effective degrees of freedom, and is therefore a straight linear relationship. This linear function is positive west of the central curtain and negative east of the east of the central curtain (Figure 3.3a). This indicates individuals released at the East and West curtains were likely to be detected at the central curtain. The smoothed term for month had 1.985 effective degrees of freedom indicating cyclic seasonal variation. In winter (months 5–7) there was a small offset eastward and

southward, to the average displacement from the release point by 2 km; the converse was true in summer (Figure 3.3b).

Table 3.1 Candidate General Additive Mixed effect linear Models of factors influencing along-slope displacement from release point of tagged *Centrophorus zeehaani* off southern Australia ranked in descending order of best fit (increasing AIC).

Model	Degrees Freedom	AIC[(a)]	ΔAIC[(b)]
displacement ~ release long[(c)] + month + habitat, random tag	6	39832	0
displacement ~ release long + month, random tag	5	39834	2
displacement ~ release long + month + length, random tag	6	39837	5
displacement ~ month + release long, random tag	5	39844	13
displacement ~ month + release long, random tag	5	38844	13
displacement ~ release long + month + moon	6	57045	7214
displacement ~ release long + month	4	57051	7220

(a) Akaike's Information Criteria, (b) change in AIC from best fit, (c) release longitude

Table 3.2 Best fit mixed model of east west displacement from release point (km) by tagged *Centrophorus zeehaani* off southern Australia
(n = 59 individuals, sum of 6053 daily observations).

Parameter	Co-efficient ± SE[(a)]	F statistic	P-value
Intercept	-6.81 ± 4.10 km	2.760	0.097
Release habitat	0.981 ± 4.42	0.200	0.842
Smooth terms	EDF[(b)]	F statistic	P-value
Release longitude	1.000	6.756	**<0.001**
Month	1.985	0.982	**<0.001**

(a) Standard error. (b) Effective Degrees of Freedom (degree of nonlinearity in the smooth term with EDF =1 being a straight line). Negative values indicate positions west of the release point. Significant P values (<0.05) are in bold. Random effects are described in Figure 3.3 c

The distribution of random individual effects on along-slope displacement is dominated by small offsets of -5 – +10 km, corresponding to movements from release points to adjacent curtains (Fig. 3c). Secondary peaks are evident at -19 and +20 km. These effects correspond to more distant movements to the East and West curtains in particular. These peaks suggest effects that are not random but are influenced by the spacing of receivers, which is wider than the typical distance travelled on the daily timescale.

Co-incident patterns in individual movement along-slope can be examined by plotting longitude against day for individual sharks (Figure 3.4). For some individuals there is evidence of movement across the closure with possible departure from the closure to the east followed by a return and movement to the west later in the study.

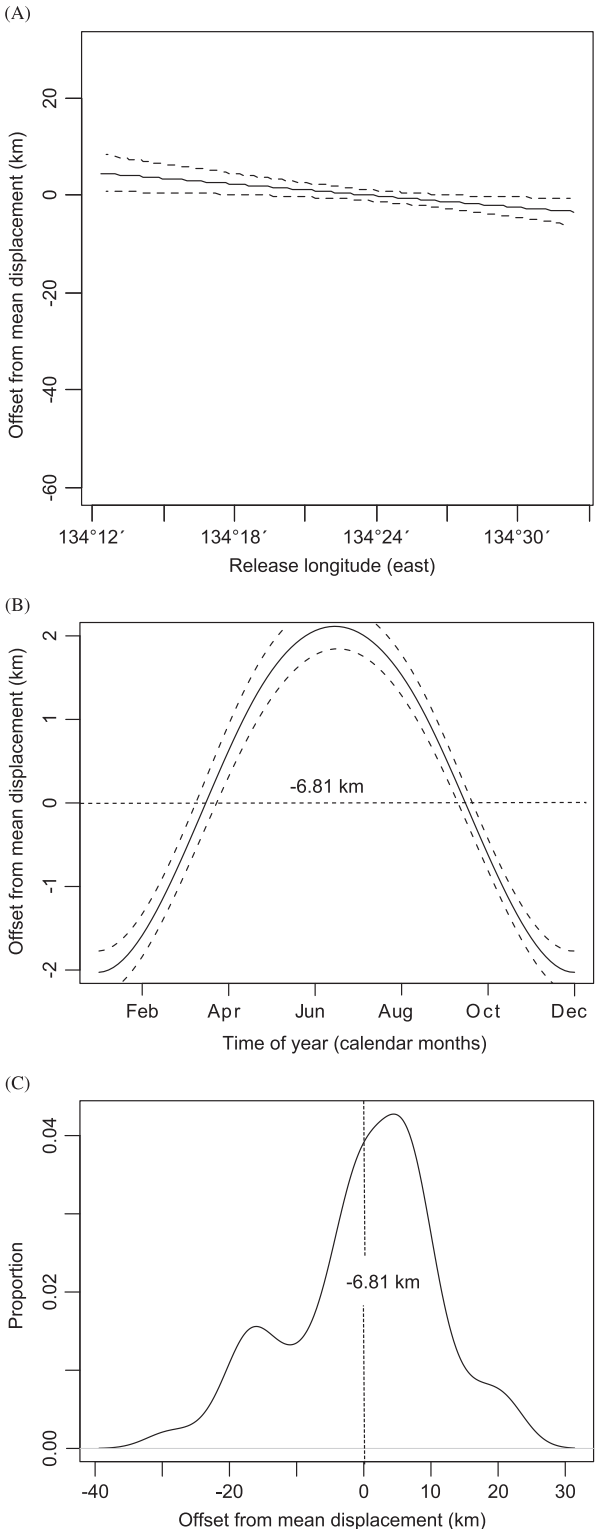


Figure 3.3 Factors affecting displacement along-slope (longitudinal) from release point of *Centrophorus zeehaani* within the receiver array.
Offset from mean displacement due to: (a) release location, (b) season, and (c) distribution of random individual effects (n = 59 individuals, sum of 6053 daily observations). Displacement is the detection location of tagged individuals in relation to their release point, negative values are towards the west. Dotted lines show 95% confidence intervals. Zero on y axis of a-b and x axis of c = -6.81 km as estimated by model intercept and estimated average displacement.

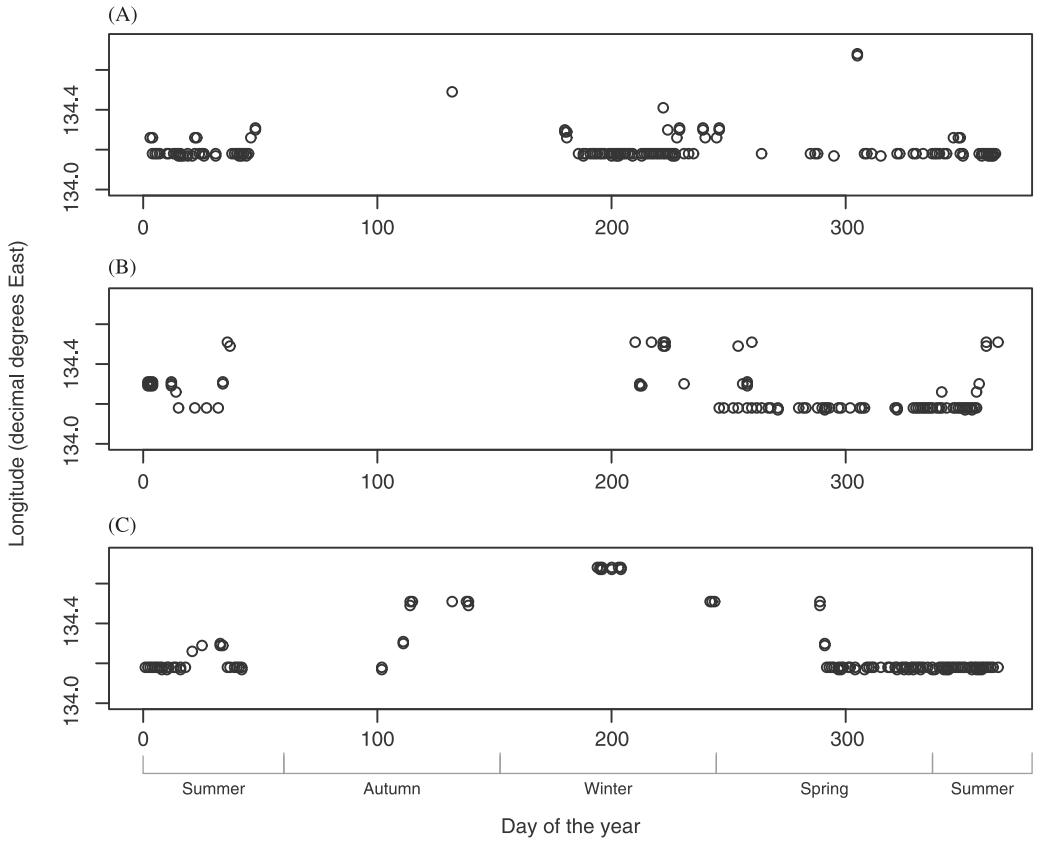


Figure. 3.4 The longitudinal movement of three individual male *Centrophorus zeehaani* within the receiver array off southern Australia showing non-coincident patterns. Some gaps in detections following easterly movements where sharks appear to leave the array and then return (a) shark #751 (b) shark #736 (c) shark #782.

Movement across-slope (depth)

The hourly (diel) filter selected 28,875 unique combinations of tag and hour. A series of six candidate depth models were developed (Table 3.3). The simplest used depth as a response to a smoothed function of hour and month with tag number as a random effect. This candidate performed poorly (ΔAIC > 500) compared to candidates with additional factors. Adding moon cycle improved the model (lower AIC). Adding habitat improved the model significantly; adding length also improved the model slightly.

The candidate with the lowest AIC was chosen as the preferred model (Table 3.4). This model was complex, including smoothed functions of hour, moon cycle and month, as well as habitat, length and tag. The intercept and overall mean depth was -487 m (Table 3.4, Figure 3.5). On average, the shallowest depths were -340 m recorded at hour 15 (3AM) (Figure 3.5a). Conversely the deepest dives were, on average to -640 m recorded at 3PM. This smoothness of the diel pattern is partly constrained by the cyclic cubic regression of the hour

function, but the very narrow 95% confidence intervals indicate this is a realistic description of the pattern.

Table 3.3 Candidate General Additive Mixed effect linear Models of factors influencing depth of tagged *Centrophorus zeehaani* off southern Australia ranked in descending order of best fit (increasing AIC).
All candidate depth models included acoustic tag ID as a random effect.

Model	Degrees Freedom	AIC[(a)]	Δ AIC[(b)]
Offset depth ~ hour + month + moon + habitat + length	10	330361	0
Offset depth ~ hour + month + moon + habitat	9	330363	2
Offset depth ~ hour + month + moon + length	7	330839	478
Offset depth ~ hour + month + moon	6	330840	480
Offset depth ~ hour + moon + month	6	330840	480
Offset depth ~ hour + month	5	330909	548

(a) Akaike's Information Criteria, (b) = change in AIC from best fit. Offset depth is the difference from the mean depth of 487.15 m.

Table 3.4 Best fit mixed model of individual depth (m) through time for tagged *Centrophorus zeehaani* off southern Australia
(n = 59 individuals, sum of 28875 hourly observations).

Parameter	Co-efficient ± SE[(a)]	F statistic	P-value
Intercept	-487.15 ± 11.97 m	1656	**<0.001**
Habitat	-34.94 ± 3.2	-10.8	**<0.001**
Length	1.75 ± 1.96	0.89	0.372
Smooth terms	EDF[(b)]	F statistic	P-value
Hour	2.00	5.04	**<0.001**
Month	1.99	1.06	**<0.001**
Moon	1.94	0.98	**<0.001**

(a) Standard Error. (b) Effective Degrees of Freedom (degree of nonlinearity in the smooth term with EDF = 1 being a straight line). Moon 0 and 100% = full moon, 50% = new moon. Significant P values (<0.05) are in bold. Random effects are described in Figure 3.5d.

During winter (months 6–8) when nights are longer, the ascents were on average into waters 20 m shallower (Figure 3.5b). The 95% confidence intervals on the seasonal function are narrow, indicating a consistent pattern over the 15 months of the study. Moon illumination had only a small influence on depth. Near the full moon (0% and 100% illumination cycle), depth was on average 5 m deeper than the mean (Figure 3.5c). Conversely at around 50% cycle, when there is less moonlight, average depth was 5 m shallower than the mean. The effects of habitat are associated with the depth of the seafloor. When traversing the ridge, depths are on average 34.9 ± 10.8 m shallower than they would be at a given hour, but this is because the seafloor prevents a deeper passage.

The distribution of random effects shows high variation due to individual preference in the mean depth occupied (Figure 3.5d). This can be further considered by examining the diel patterns of individuals. The random effects were dominated by eight individuals, four with mean depths of 630 m or deeper and four with mean depths 330 m or shallower. Although

these eight individuals occupied unusual depth ranges, their overall diel profiles were similar to the model (Figure 3.5a). This suggests that all individuals have the same diel pattern but at different parts of the seafloor, including areas that are mainly deeper and shallower than the array.

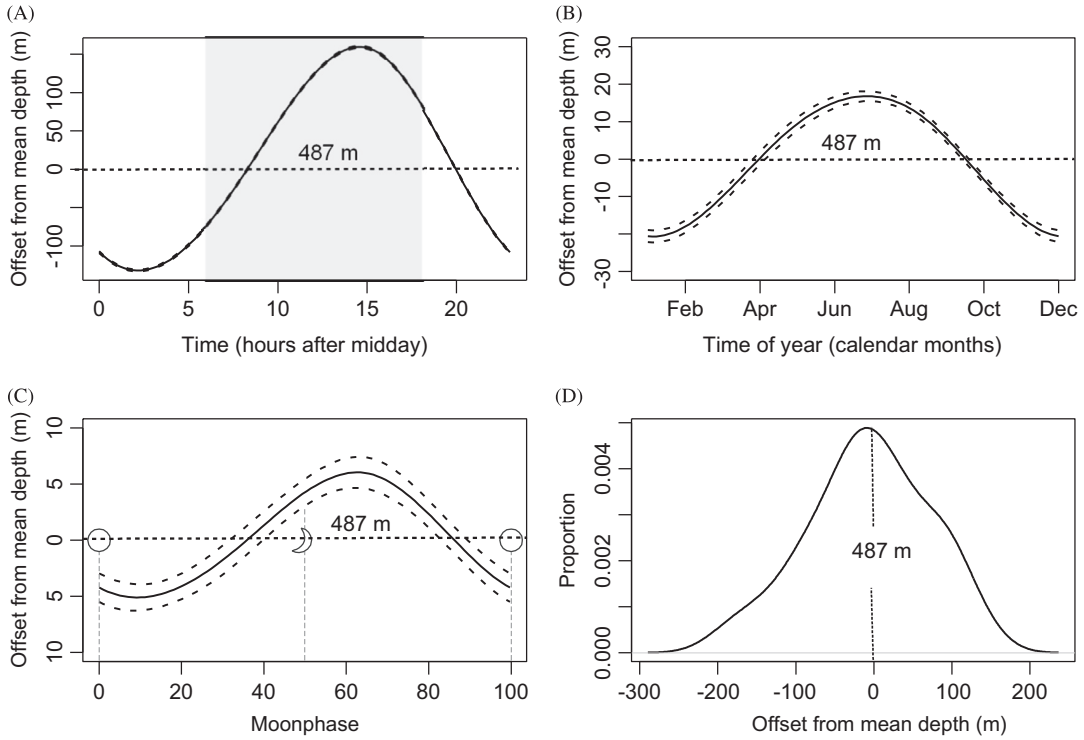


Figure 3.5. Factors affecting change in depth of *Centrophorus zeehaani* within the receiver array off southern Australia.
Offset from mean depth due to (a) time of day (diel migration), (b) season, (c) moonphase (0 and 100% = full moon, 50% = new moon), (d) distribution of random individual effects (n = 59 individuals, sum of 28875 hourly observations). Dotted lines show 95% confidence intervals. Zero on y axis of a-c and x axis of depth = 487 m as estimate by model intercept and estimated average depth.

A change in depth can reflect movement in the water column or movement across the sloping seafloor. The linear regression of the detection depths as a response to seafloor depth at receiver was highly significant ($P < 0.001$, $R^2 = 0.5762$) with a slope of 1.01 and a y-intercept of -11.5 m (Figure 3.6). This resulting mean indicates *C. zeehaani* on average passed the receivers near the seafloor. The variance around the mean was high indicating some of the movements must have been further down the slope below the receivers and some were either inshore or into the water column shoreward of the receivers.

3.4 Discussion

Acoustic receiver array

The across-slope curtain-array configuration chosen for this study was a compromise between assessing the performance of the fishery closure and examining the ecology of *Centrophorus zeehaani*. Gridded arrays are an alternative with the potential to provide greater insights into habitat use, but generally these have been deployed over much smaller scales, (Heupel, Semmens *et al.* 2006). Strategically placed curtains can be used to determine when animals enter or leave an area (Lacroix, Knox *et al.* 2005), and this was our intention. The very narrow continental slope was amenable to a curtain design as the species' depth range could be covered by 3–4 receivers and proved to be especially well suited to measuring the shark's diel pattern of vertical migration. However, the loss of some receivers created uncertainties. These uncertainties were addressed by careful consideration of the statistical analysis.

Statistical analysis

The loss of some receivers limited the understanding of residency that could be gained from the four summary metrics. Duration tended to be high but daily residency tended to be low. This contrast suggests that *C. zeehaani* typically took several days to move between receivers and/or moved past curtains without being detected. This could have occurred as sharks moved past curtains where receivers were lost (Figure 3.1), or to seaward of the array during deep dives. These problems were partly addressed by using a coarser (monthly) time scale to examine male and female residency. The number of males detected per month decreased during the study. This suggests at least some of the males were non-resident, moving outside the closure area and not returning during the study period.

The GAMM model framework compensated for the loss of receivers much better than the simple summary metrics. The GAMM's smoothing functions accounted for movements in relation to daily, lunar and seasonal patterns in both along-slope and across-slope models. We had no prior knowledge of movement rates of deep-sea sharks to help determine optimal receiver spacing, and the performance of the linear model of along-slope movement was partly limited by the wide spacing of curtains. A closer spacing of receivers is conservative, and may be more appropriate for telemetry studies in the deep sea where there is a risk of data gaps due to gear that cannot be recovered. Hobday and Pincock 2011 used statistical methods to account for the likelihood that individual tuna could pass a receiver in a linear longitudinal array without being detected. However, individual movement simulation models may be needed to represent broader scale movements of deep-sea species that have complex diel

rhythms superimposed on unpredictable along-slope movements with periods of local residency.

Tagging, survivorship and data quality

The success of any tagging study is highly dependent on survivorship of the tagged individuals. Pressure changes associated with capture can contribute to barotrauma in teleosts with gas-filled swim bladders and special techniques are needed to limit mortality (Parker, McElderry *et al.* 2006; Wassenberg and Hill 1993). Chondrichthyans lack swim bladders but buoyancy is regulated by liver oils, which can also be sensitive to pressure changes (Pethybridge, Daley *et al.* 2010; Phlegar 1988). Adult *C. zeehaani* had high rates of survivorship in this study. Even though sharks showed signs of stress during capture, the tag transmission patterns suggest normal behaviour resumed following release when handled carefully. The great majority of the tagged individuals were subsequently detected at varying depths suggesting they had resumed moving actively. However, 11 *C. zeehaani* were never detected, and there are at least two possible explanations. These sharks died or moved out of the listening station array prior to reaching a detection depth. It is possible that buoyancy regulation was compromised by the effect of pressure change on the liver.

Residency and along-slope movement

The residency results have key implications for evaluating the efficacy of the fishery closure in relation to its size. Previous studies indicated the sustainable yield (fishing mortality) of *C. zeehaani* populations is exceptionally low, within the range of 3–5% of biomass (Forrest and Walters, 2009). The monthly residency analysis in this study indicated that 39–65% of males left the fishery closure and did not return during the study period of 15 months. Outside the closure they are potentially exposed to fishing methods (bottom trawling and bottom-set longlining) that will result in high mortality rates of captured individuals. Over the same period, there was not a significant decline in the number of females. The potential loss of some males may not be critical if not all males in the population mate successfully. Nonetheless, the along-slope results provide insights for understanding when and how *C. zeehaani* leaving the closed area may interact with fishing activities, and for identifying the potential for complimentary fishing regulation such as seasonal restriction in fishing near the closure boundaries. Some individual sharks were more likely to move east during winter than others (Figure 3.4). Data on movements outside the closure, or simulation models, would be useful to evaluate the potential of fishing effort controls near the eastern margin of the closure area to reduce bycatch of non-resident individuals

The extent that mortality of non-resident individuals outside the closure area impacts on the population size is difficult to assess due to a number of uncertainties. Catch data indicate *C. zeehaani* segregate by sex (Graham and Daley 2011). The timing of any movements associated with mating is difficult to predict because the female cycle of *C. zeehaani* is aseasonal, asynchronous and likely to last 2–3 years (Graham and Daley 2011; McLaughlin and Morrissey 2005), which is longer than the duration of this study. Some inferences can be made by considering other species. Sex-based dispersal is well known for some species of sharks from the continental shelf, e.g. white sharks and scalloped hammerhead sharks (Blower, Pandolfi *et al.* 2012; Daly-Engel, Seraphin *et al.* 2012; Pardini, Jones *et al.* 2001). Similarly, female whaler sharks have been shown to have seasonal shifts in habitats and depths (Knip, Heupel *et al.* 2012). Length frequency and sex ratio data from the closure population of *C. zeehaani* is needed inside and outside the closure to support interpretation of likely patterns of male and female residency.

Movement Across-slope (depth-related) movement

Movements of *C. zeehaani* appear to be highly influenced by variation in ambient light levels, as evidenced by a pronounced diel migration with lunar and seasonal cycles superimposed. Diel vertical migration is a feeding strategy to exploit the deep-scattering layers of micronekton – diverse oceanic communities of small fishes, crustaceans and squids that impinge upon continental slopes, including off temperate Australia (Williams and Koslow 1997). For predators such as *C. zeehaani* that feed on micronekton (Graham and Daley 2011), the night time ascent of these layers and their concentration at shallower (< 400 m) slope depths at night compared to day (> 400 m) (Williams and Koslow 1997) is undoubtedly a major driver of *C. zeehaani* movement. Unlike abundant co-occurring diel vertical migrating species such as the blue grenadier or hoki (*Macruronus novaezelandiae*) that ascend in the water column, the linear relationship between tag depth and seafloor depth at receiver shows that movement of *C. zeehaani* was typically near the seafloor (i.e. they were moving up and down the slope).

Individual hourly data showed that, despite otherwise similar synchrony in diel patterns, individual sharks occupied slightly different depth ranges, with some individuals being relatively deep or relatively shallow dwelling. The extent of diel ascent was, on average, shallower with longer nights and less moonlight. This perhaps suggests that *C. zeehaani* uses the cover of darkness to maximise its interaction with the highest concentrations of micronekton biomass, which also undergoes diurnal vertical migration –ascending to < 300 m off the temperate coast of southern Australia and descending during the day (Williams and Koslow 1997). Enclosing the night time (shallow) distribution of diel migrating species is a

key consideration for fishery closure design. The shallow boundary of this closure at the continental shelf edge (< 200 m depth) encompasses the shallow limit of C. zeehaani, and in this regard mitigates the effects of fishing on *C. zeehaani*.

Conclusions

Our study demonstrated that a species of deep-sea shark can be monitored using passive acoustic telemetry. The handling practices developed in this study limited stress levels and minimized mortality. Most of the female *C. zeehaani* tagged in the fishery closure off southern Australia were resident whereas males were more likely to be non-resident. The effect on population size resulting from incomplete residency within the closure is difficult to predict due to two key uncertainties: a lack of movement data from outside the closure, and limited knowledge of the female breeding cycle.

For *C. zeehaani*, the effects of sex on residency and along-slope movements were complicated by high variation in patterns between individuals. Most of the mature (based on size) females tagged within the closure were resident during the study. The shallow boundary of this closure is effective for protecting *C. zeehaani* because it fully encompasses the shark's shallow limit of diel movement. The clear diel pattern of vertical migration with monthly and seasonal signals appears to be a response to light and linked to feeding on migrating micronekton.

Care is needed when applying the results to other species. In the absence of detailed knowledge of the breeding demographics and feeding patterns of other species in the closure, residency will be largely uncertain.

CHAPTER 4. MARINE SPATIAL MANAGEMENT OPTIONS FOR DATA POOR VULNERABLE MARINE SPECIES

4.0 Abstract

We used a participatory management strategy evaluation (MSE) approach to lay bare and evaluate the trade-offs between resource use and conservation objectives in marine spatial management for data poor vulnerable species. Two deep-sea shark species managed by fishery closures in Australia were used as a case study. Participants included fishers, scientists, fishery managers, and government and non-government conservation groups. The broad conservation objectives were to halt decline and support recovery of previously depleted populations. Competing resource use objectives were to limit lost catch for commercial species and displaced fishing effort. Key uncertainties included population structure, abundance, release survivorship and mobility. Semi-quantitative criteria were developed to measure performance of marine spatial management options against objectives at local and national scales, taking key uncertainties into consideration. At the local scale, survey data were used to develop relative abundance and breeding success criteria that were better able to predict efficacy of protection than simple area measurements. Fishery stakeholders who understood these criteria, recorded catch locations with precision, and provided additional data. They contributed most to the process and were in a better position to later negotiate the trade-offs. At the national scale, three criteria were used to evaluate the efficacy of the closure networks for each species to maintain genetic diversity, and provide resilience against localised impacts (e.g. an oil spill) and wide spread ecological change (e.g. ocean temperature change) over decades. Scientists were able to play a policy-neutral role, coordinating the evaluation and aiding communication between the various jurisdictions. Two closure networks were implemented. Flexible and adaptive management has subsequently revised the networks in response to additional monitoring data, changes in species protection regulations, and providing better integration with Commonwealth marine reserves. The approach adopted has wider relevance for considering trade-offs in conserving marine species where data are poor and uncertainty is high.

4.1 Introduction

The adoption of ecosystem approaches to managing marine industries under national and international agreements provides broad mandates to identify and conserve vulnerable marine species. This responsibility has long been recognized by fisheries agencies but becomes problematic where low productivity species co-occur as bycatch of fisheries targeting higher productivity commercial fish species (Hilborn, Branch *et al.* 2003). Adverse events such as oil spills also raise concerns with other industries as they expand deeper in the marine environment. It has been argued that the loss of the most vulnerable marine species is unavoidable (Brander 1981). Such species are useful for exploring the challenges of managing the trade-offs between resource use and conserving marine biodiversity.

Recent ecological risk assessments have identified some deep-sea sharks as being at higher risk from human activities than most seabirds or marine mammals (Gallagher, Kyne *et al.* 2012; Hobday, Smith *et al.* 2011). Of world-wide concern are species in the genus *Centrophorus,* a group of medium sized (0.7–1.7 m) demersal sharks widely distributed on the continental slope in the world's oceans (Daley, Williams *et al.* 2015; Kyne and Simpfendorfer 2010). These species exemplify the typical attributes of k-strategists, an adaptation to the stable deep-sea environment. Their productivity is amongst the lowest of known vertebrates. Some species have only 1–2 pups born live after 2–3 years gestation that do not mature until 17–24 years of age (Graham and Daley 2011; McLaughlin and Morrissey 2005; Whiteley 2008). For some species, ecological risk is increased by restricted geographic and bathymetric distribution that limits available habitat (Daley, Williams *et al.* 2015) (Chapter 3).

Fishing has depleted six species of *Centrophorus* in the northeast Atlantic, southwest pacific and Indian Oceans (Adam, Merrett *et al.* 1998; Graham, Andrew *et al.* 2001; ICES 2010). Although measures have been introduced to end targeted fishing in the northeast Atlantic and off south-eastern Australia, these species are still taken as bycatch in multi-species trawl and auto-longline fisheries. (Forrest and Walters 2009; ICES 2005).

Off southern and eastern Australia, two species *C. harrissoni* and *C. zeehaani* have been extirpated from key parts of their range, particularly off southern New South Wales, leading to national scale protection in Australia (Environment 2013; Graham and Daley 2011; Kyne and Simpfendorfer 2010). Both state and federal bodies share responsibility for their recovery because the distributions of these species extend over jurisdictional boundaries. Marine spatial management, including areas closed to fishing, was implemented to 'halt declines' of these species in 2005 and was later expanded to 'support recovery' in 2012 and 2013 (AFMA

2013a, b) (Figure 4.1A). Australia also has a network of Commonwealth marine reserves that were implemented with broad biodiversity conservation aims and that also have some potential to contribute to the conservation of gulper sharks (Williams, Althaus *et al.* 2013).

Size, placement and spacing are critical factors in designing closures that are effective in managing fish populations impacted by fisheries (Sale, Cowen *et al.* 2005). Successful implementation of marine spatial management requires understanding and management of edge effects of fishing in particular; that is incidental mortality just outside closures. These effects arise where individuals have home ranges partly inside and partly outside closures. The larger the home range, the greater the edge effects, and the larger the closures need to be to buffer against them. Limited data on species distribution, abundance and patterns of movement made it difficult to evaluate these factors objectively for *Centrophorus* in Australia.

Management strategy evaluation (MSE) is a framework for assessing consequences of applying alternative management strategies in a way that lays bare the trade-offs across a range of competing management objectives (Smith, Sainsbury *et al.* 1999). It is also a way of formally taking account of scientific uncertainty associated with data poor species in providing this information. In other words MSE is a decision support tool to assist in making decisions between alternative courses of action where there are conflicting objectives and where there is significant scientific uncertainty in predicting outcomes.

MSE methods have been widely applied in fisheries, mainly to evaluate the performance of different harvest strategies for target species (Smith, Smith *et al.* 2008), but also to evaluate overall strategies for managing the fishery to reconcile economic and ecological outcomes (Fulton, Smith *et al.* 2008; Fulton, Smith *et al.* 2014; Smith, Fulton *et al.* 2007). MSE mostly uses quantitative models to predict the outcomes of applying a particular strategy, but has also used qualitative methods (expert judgment) and this was found to predict outcomes quite well relative to the more quantitative methods (Smith, Sachse *et al.* 2009; Thébaud, Ellis *et al.* 2014).

Here we outline a semi-quantitative MSE framework developed to evaluate spatial management options for data poor vulnerable marine species. We describe the evaluation of *C. zeehaani* and *C. harrissoni* in Australia as examples using catch and effort survey data and other limited information. We discuss how uncertainty is considered during evaluation and implementation of results. We also discuss how scientists can help co-ordinate the process

and inform discussion between agencies that manage fisheries and conservation aspects of the same species.

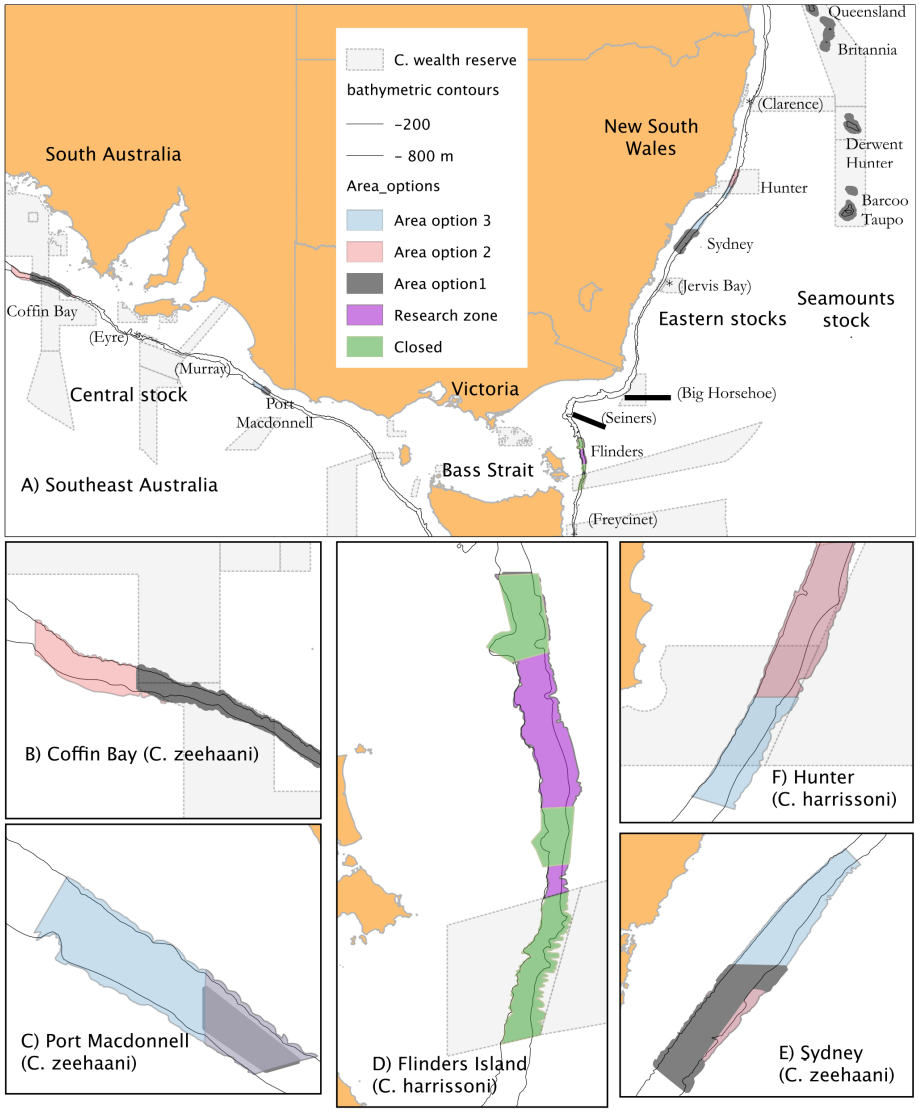


Figure 4.1 Area options considered for *Centrophorus* off Southeastern Australia. Locations in parentheses scored poorly in screening stage 1. Western stock of *C. zeehaani* is not shown.

4.2 Methods

The MSE proceeded in 5 steps: 1. Identify all relevant objectives. 2. Consider existing knowledge and key uncertainties – stating all assumptions 3. Identify criteria for measuring performance against objectives. 4. Choose a set of management options to evaluate. 5. Predict how each option would perform against each of the criteria.

Objectives

We took the overarching conservation objective from the fishery management plan to be 1. "halt declines" and 2. "support recovery" of *C zeehaani* and *C. harrissoni*. We took the overarching economic efficiency objectives for the relevant fisheries to be maximising economic returns, approximated by minimizing the loss in the gross income (catch) value as a result of closures, and limiting the amount of fishing effort, and associated key costs, that would have to be shifted from areas selected for closure to alternative fishing areas (Australia 1991).

Key knowledge and uncertainties

Data limitations for the two species in question presented four key uncertainties: 1. The number of demographically independent populations and their geographic boundaries were not known; 2. Data on relative abundance and the spatial distribution of key demographic components including breeding adults/mating areas and juveniles/nursery areas were unclear; 3. Survival rate following capture and release was uncertain and 4. Knowledge of mobility (home range and movement) was based on only one study of *C. zeehaani* (Daley, Williams *et al.* 2015) (Chapter 3). An Upper Slope Dogfish Scientific Working Group (USDSWG) was formed to answer a series of questions from the federal department of conservation and met to review those uncertainties (Williams, Althaus *et al.* 2013).

In the absence of detailed genetic data on population structure, the USDSWG used breaks in the spatial distribution of catch data to identify three likely populations of *C. zeehaani* breeding independently around the continental margin of temperate southern Australia: 1. Eastern, 2. Central, 3. Western (Figure 4.1A) (Williams, Althaus *et al.* 2013). Adults live mainly near the seafloor between the 200–650 m bathymetric contours in temperate waters (Daley, Williams *et al.* 2015) (Chapter3). Survey catch data suggest that Bass Strait and high latitudes around Tasmania that are less than 100 m deep form a barrier to dispersal between the eastern and central populations; similarly low latitudes west of Coffin Bay form a barrier to dispersal between the central and western populations for this temperate species (Figure 4.1). The USDSWG assumed two putative Australian populations of *C. harrissoni*: 1. Eastern

(continental), and 2. Remote seamounts (Figure 4.1A) (Williams, Althaus *et al.* 2013). Given this species has only been caught between the 275–1050 m bathymetric contours (Graham and Daley 2011), the expanse of open ocean 125–321 km wide that is deeper than 1,500 m between the eastern continental margin of Australia and the remote seamounts is a likely to be a barrier to dispersal between these two populations.

Effective reserves for sharks and rays need to contain juveniles and breeding males and females in sufficient abundance at the same location (Dulvy and Forrest 2010). Relative abundance, sex ratios and length frequencies were calculated for this study from existing commercial and survey hook and line catch and effort data collected from 25 locations around south-eastern Australia (Williams, Daley *et al.* 2012).

As bycatch species, most individual *Centrophorus* are alive when caught on auto-longlines but dead when caught by trawl (due to crushing). For auto-longlines, survivorship is uncertain but within the range of 22–93% (Daley, Williams *et al.* 2015; Williams, Althaus *et al.* 2013) (Chapter 3). The USDSWG considered that these survivorship rates meant that potential restrictions on auto-longlines did not need to be as strict as for trawl, but this needed more research.

Matching closure options to the mobility of species to be managed is critical to effectiveness (Awruch, Frusher *et al.* 2012; Sale, Cowen *et al.* 2005). Closures are most likely to be effective for shark species with individual home ranges of intermediate scales: tens of km wide (Bonfil 1999). A recent electronic tagging study of *C. zeehaani* identified individual males that moved more than 50 km along the slope in one year, whereas females tended to move less than 10 km (Daley, Williams *et al.* 2015) (Chapter 3). The same study found that individual *C. zeehaani* undertake diurnal movements across the slope near the seafloor, moving towards the shore and reaching the 200 m bathymetric contour at night, and returning to near the 650 m contour each day. There are no such studies for *C. harrissoni* but the bathymetric range for this species was determined from survey catch data to be 275–1050 m (Graham and Daley 2011). For both species, the continental slope forms a steep narrow strip of habitat off much of southern Australia (Last, Lyne *et al.* 2010).

Selection of criteria and options

A total of nine conservation criteria were selected and applied to both species separately in three stages to: 1. Short-list candidate areas (locations), 2. Evaluate the performance of alternative area options for shortlisted areas, and 3. Ensure that the closures would integrate into larger-scale networks that would achieve recovery over generations. Stages 1 and 2

consider management of populations under single management jurisdictions (state or federal) at local scales: 10–100 km; Stage 3 considers overall species conservation at regional scales: 1,000–3,000 km, requiring cross-jurisdictional management arrangements.

In Stage 1, candidate areas were identified during discussions between fishery and conservation stakeholders and government agencies (Graham and Daley 2011; Williams, Daley *et al.* 2012). Three leading conservation criteria were then used to short-list areas (Table 4.1). 'Relative abundance' was scored based on semi-quantitative thresholds from hook and line fishery and survey catch data: number of individuals/100 hooks (Graham and Daley 2011; Williams, Daley *et al.* 2012). A catch rate >0.1/100 hooks was needed for a medium score, >1 for a high score. 2. 'Breeding success' is a conditional criterion that uses proxies for mating locations (adult males and females present) and pupping locations (juveniles present) based on the survey data. At least one condition must be met for a medium score, both for a high score. 3. 'Proximity' is a categorical criterion based on the measured distance from a candidate area to the nearest location where the relevant species has been recorded in recent survey data. A distance of <50 km is needed for a medium score, <25 km for a high score. At the end of stage 1, only areas that scored med or high for criteria 1 and 2 and high for criterion 3 were selected to proceed to stage 2.

In stage 2, stakeholders contributed area options for the short listed areas. Area options varied the size and boundaries for a given area (Figure 4.1 B–F). This stage used criteria 1–3 supplemented by three additional conservation criteria (Table 4.1). Criterion 4 'Habitat condition' acknowledges heavy historical fishing by trawl and (to a lesser extent) auto-longline gear can damage habitat by removing attached fauna (Daley, Webb *et al.* 2006; Wayte, Dowdney *et al.* 2006). This measure was based on the sum of trawl and line effort obtained from fishery logbook data as well as survey data if available. Criterion scores were classified to high, medium and low by expert judgment of benthic ecologists, taking into account differential impacts of the gears and the habitats they could access.

Criterion 5: 'Range along-slope' (around the continent) and 6: 'Range across-slope' (seafloor depth – on/offshore), measure the likelihood that a given area option will correspond in scale to the mobility of individual sharks. For *C. zeehaani*, thresholds were based on published data (Daley, Williams *et al.* 2015) (Chapter 3). Key knowledge and uncertainties are described above. For *C. harrissoni* the across slope range was estimated based on survey data (Graham and Daley 2011) and the along slope range was assumed to be similar to *C. zeehaani*.

Table 4.1 Scoring criteria and thresholds for management strategy evaluation of vulnerable species.

Criterion	Metric	High	Med	Low
Area Options				
1. Relative abundance	% Catch rate	>1	0.1–1	<0.1
2. Breeding success	Demographic components	2	1	0
3. Proximity	Distance to area (km)	< 25	25–50	> 50
4. Habitat condition	Impact (Expert)	Heavy trawl or auto-longline	Moderate both methods	Light both methods
5. Range along-slope	Linear distance (km)	>80	50–80	<50
6. Range across-slope	Bathymetric contours (m)	200 - 700	NA	< 200 - 700
Closure networks				
7. Extent of occurrence	Proportion of pre-fishery latitudinal, longitudinal range	> 50% of latitude and longitude	> 50% of latitude or longitude	<= 50% of latitude and longitude
8. Area of occupancy	Sum of area (km^2)	<1250	1250–2500	>2500
9. Genetic diversity	Number of closures/ population	>1	1	<1
Economics				
10. Cost of lost catch	Annual average catch of quota species 2008–12 (t)	>50	10–50	<10
11. Displaced effort	Average no. operations per year: 2008–12	>100	20–100	<20

Network options at the National scale need to consider that over the 63 years needed for recovery (Chapter 5), one or more closed areas/populations could become unviable due to human or natural localised impacts – e.g. a single oil spill. Three conservation criteria were used: 7. 'Extent of occurrence' aims to maximise both the latitudinal and longitudinal range of a network with respect to the un-fished species range to buffer against long term changes over large scales, such as sea temperature change. A medium score requires the network to cover the full latitudinal range or longitudinal range of a population, both for a high score. 8. 'Area of occupancy' is a proxy for carrying capacity, and is measured as the sum of the areas

protected, calculated using the 'Quantum' GIS package. 9. 'Number of closures per population' is a proxy for 'genetic diversity', where the areas are those assumed to represent separate populations separated by barriers to dispersal (see key uncertainties above). At least one closure for each population is needed for a medium score, >1 closure per population for a high score.

Two economic criteria were used to quantify the potential costs to industry and applied to options at both stages 2 and 3 (Table 4.1). Criterion 10: 'Cost of lost catch' is a proxy for the cost due to lost yield of closing an area to fishing and was based on the annual average gross production (landed) value for the key target species in the fishery for the period 2006–2010 inclusive. Criterion 11: 'Displaced fishing effort' is a proxy for cost based on the average of the sum of fishing operations in each area for 2006–2010 inclusive. Criteria 10 and 11 were expressed quantitatively for the federal trawl fisheries impacted by the closures, but qualitatively for the auto-longline fisheries (which have a smaller fleet with stricter confidentiality arrangements about publicly reporting catch and effort).

4.3 Results

Stage 1: Candidate areas and shortlist

A total of 13 candidate area locations were considered at the start of stage 1 screening (Figure 4.1A). Ten candidate areas were species-specific. These represented *C. zeehaani* central population: Coffin Bay, Eyre, Murray, Port MacDonnell; *C. zeehaani* eastern population: Freycinet, Sydney; *C. harrissoni* eastern continental population: Flinders, Hunter, Clarence; *C. harrissoni* seamounts population: remote seamounts. Three candidate areas had some potential for populations of both species: Seiners, Big Horseshoe, and Jervis Bay. The *C. zeehaani* western population could not be included because the relevant fishery data did not have sufficient spatial resolution and surveys were unable to locate the population (Williams, Althaus *et al.* 2013).

Of the 13 candidate areas (Figure 4.1A), 7 were excluded by applying the criteria at Stage 1. The exclusions included three areas known by industry to have previously held populations and considered suitable habitat and within the range of both species, but recent survey data found a lack of abundance, breeding success or proximity to other populations: Seiners, Big Horseshoe and Jervis Bay. The other four exclusions were areas in or adjacent to proposed CMRs: Eyre, Murray, Freycinet and Clarence. Fishery records show these areas have historically held populations of *Centrophorus* species, and potentially could avoid duplication of closures, but there was no evidence of breeding success at these locations. The remaining

six areas were given detailed consideration in stage 2. These included three areas for *C. zeehaani*: Coffin Bay, Port MacDonnell and Sydney; and three areas for *C, harrissoni*: Flinders, Hunter and remote seamounts.

Stage 2A: Area options for C. zeehaani

Two options were developed for the Coffin Bay area (Figure 4.1A,B, Table 4.2, Figure 4.2A): the first option corresponds to an existing fishery closure; the second option added an extension of the existing closure 72 km westward along the slope.

The evaluation of the Coffin Bay Options found that option 2 would have only limited additional benefit for conservation because both options score high for all six conservation criteria. The existing fishery closure already contained high numbers of males, females and juveniles, therefore scoring high for abundance and breeding success (Figure 4.2A). The cost to industry of option 2 would be high to the auto-longline fleet but low to the trawl fleet, because much of the seafloor inside the proposed extension is rough and difficult to trawl. In contrast, the auto-longline fleet relies on fishing this area; therefore option 2 would require a substantial trade-off of lost fishery production. Option 1 was implemented in 2005 and reviewed in 2013 but not modified as subsequent surveys found that *Centrophorus* abundance had been maintained (suggesting that the closure was effective in protecting this local population).

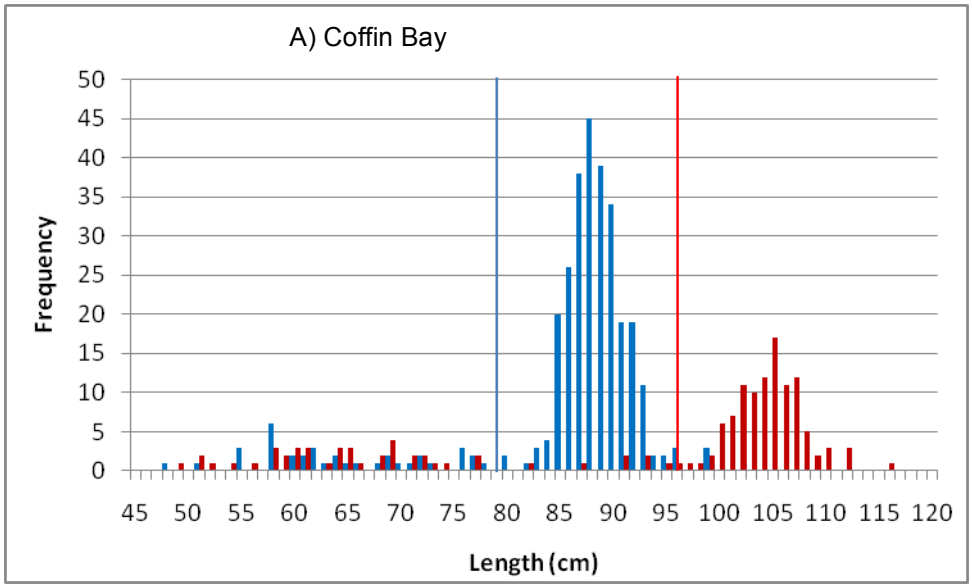
Three options were developed for the Port MacDonnell area (Figure 4.1A,C): the first was an existing fishery closure; the second extended that closure further into deeper waters; and the third extended the existing closure into deeper waters and along the slope.

The evaluation of Port MacDonnell area options found option 1 scored high for abundance but only medium for breeding success because adult females were rare in the area (Figure 4.2B). The expanded depth range of options 2 and 3 would cover the full seafloor depth range of *C. zeehaani,* limiting edge effects just outside the deepest margin of the closure. However option 2, at only 16 km in length, still only scores low for along slope range. Option 3 at 43 km in length is an improvement in this regard and scored medium for along slope range. Area options 2 and 3 at Port MacDonnell both result in substantial costs for auto-longline effort and particularly for the trawl sector, displacing 50 t/year in catch and 355 fishing operations on this historical trawl ground. Option 1 was implemented initially and modified in 2013. The modification consisted of a negotiated compromise of intermediate size between options 2 and 3 that extended the closure deeper and to a total of 57 km along the slope.

Table 4.2 Management strategy evaluation of Area options for *Centrophorus* species off southern Australia.

Area and option	Conservation Criteria						Economic Criteria			
Species Area Option	1. Abundance	2. Breeding	3. Proximity	4. Habitat	5. Along-slope range	6. Across-slope (depth) range	10A. Lost trawl catch	11A. Displaced trawl effort	10B. Lost auto-longline catch	11B. Displaced auto-longline effort
C. zeehaani										
Coffin Bay										
1. Existing	H	H	H	H	H	H	L	L	L	L
2. >length	H+	H+	H	H	H	H	L	L	H	H
Port MacDonnell										
1. Existing	H	M	H	L	L	L	L	M	L	L
2. >depth,	H	M	H	L	L	H	H	H	L	M
3. >depth, >length	H	M	H	L	M	H	H	H	L	M
Sydney, New South Wales										
1. Existing	H	M	H	M	M	M	?	?	L	L
2. >depth	H+	M+	H	M	H	M	?	?	L	L
3. >depth, >length	H+	M+	H	M	H	H	?	?	L	L
C. harrissoni										
Flinders										
1. Existing	H	M	H	M	H	L	L	L+	H	H
2. > depth	H	M	H	M	H	H	L	L+	H	H
3. > depth & closed	H	M	H	M	H	H	L	L+	H	HH
Hunter										
1. Original	?	?	H	M	L	L	?	?	L	L
2. >depth,	?	?	H	M	M	H	?	?	L	L
3. >depth, >length	H	M	H	M	H	H	?	?	L	L
Seamounts										
1. Existing (2 closed)	M	M	NA	H	NA	NA	L	L	L	L
2. Five closed	H	M	NA	H	NA	NA	L	L	H	H

L= low likelihood of meeting an objective, M= medium likelihood of meeting an objective, H= High likelihood of meeting an objective, H+ indicates high with improvement.. HH = extremely high cost to industry. Bold = difference in scoring



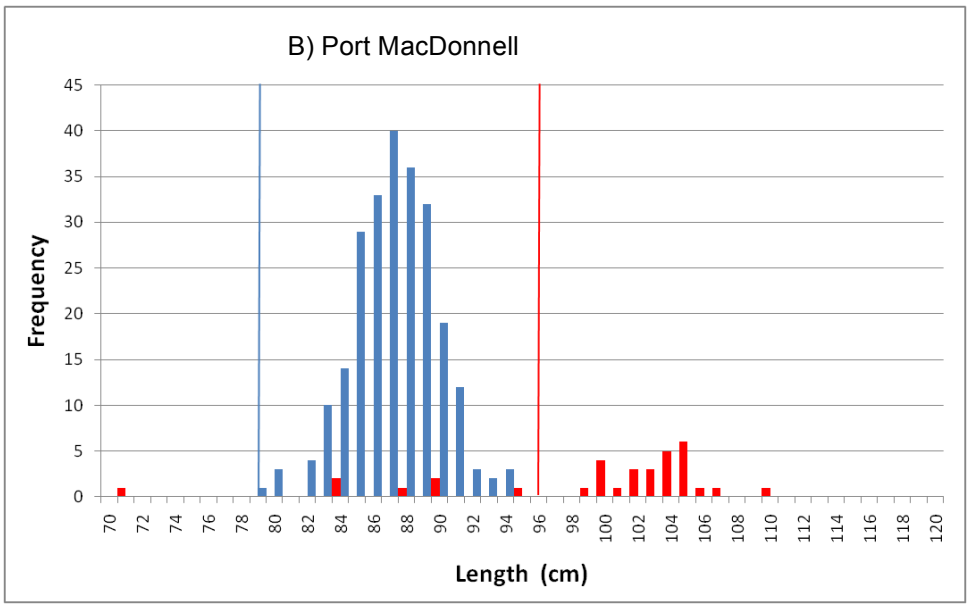


Figure 4.2 Length frequency of male (blue) and female (red) *Centrophorus zeehaani* at two areas off Southern Australia (Figure 4.1 B, C). Vertical lines indicate size at maturity. Note different horizontal scales.

Three options were developed for the Sydney area (similar to Port MacDonnell) (Figure 4.1A, E): option 1 was an existing closure (to protect undersea cables); option 2 would extend the existing closure into deeper waters; and option 3 would extend both deeper and along the slope to the north.

The evaluation found all three Sydney area options had the same scores for conservation criteria because abundance in the existing closure was high (Figure 4.3B) but low in the

proposed extension to the north (Figure 4.3A). The options differed in along-slope and across-slope range criteria scores. The extension into deeper water offered by options 2 and 3 would reduce edge effects. Option 3 increases the along-slope range substantially from 56 km (medium) to 123 km (high). The associated trade-off for trawl could not be measured because the trawl fishery catch data off New South Wales do not have sufficient spatial resolution. There is no cost to auto-longline because this fishing method has never been permitted off New South Wales. Option 2 was implemented and later expanded to option 3 in 2013 to provide greater potential for recovery.

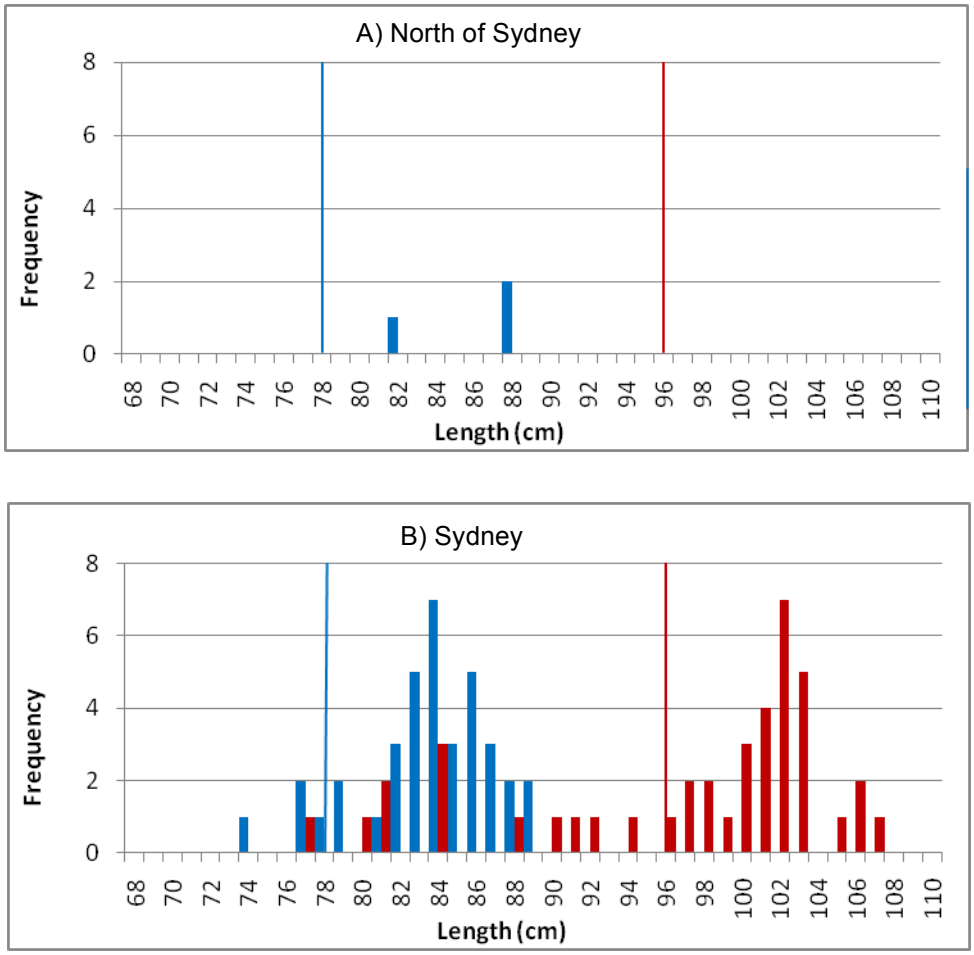


Figure 4.3 Length frequency of male (blue) and female (red) *Centrophorus zeehaani* at the Sydney area off eastern Australia (Figure 4.1 A, E). Vertical lines indicate size at maturity.

Stage 2B: Area options for C. harrissoni

Developing area options for Flinders was of key importance to conservation as the only area within the range of the eastern population containing males, females and juveniles across a manageable scale. The area was also challenging because it has high value for both trawl and auto-longline. The options considered for this area were more complex than in other areas. The complexity was needed to limit the potential costs to the extent possible.

Three options were developed for the Flinders area (Figure 4.1 A, D). These options vary the size of the closure and the permitted uses: option 1 consisted of status quo management arrangements. Since 2010 the area has been managed as a "research zone". The research zone includes two fully closed areas at its northern and southern ends. The remaining part of the zone can be fished by auto-longline only (not trawl) provided there is an observer on board. The research zone could also support further research into survivorship of released *Centrophorus* by implementing a tagging program. Option 2 extends the research zone deeper. Option 3 has the same coordinates as option 2, but is a full closure (no research fishing even with an observer).

The evaluation of the Flinders area found all three options had the same scores for 8/10 criteria. Importantly the area contained males and juveniles to the north (Figure 4.4 A, B) consistently in two consecutive years and mature females to the south (Figure 4.4 C, D). Combined northern and southern parts of the areas give a high score for breeding success, although this is not entirely certain because females were in low numbers in 2009 (Figure 4.4 C). The key differences were in the range across-slope and the cost to industry. Increasing the depth range in options 2 and 3 would reduce edge effects. A full closure would have an extremely high impact on displaced auto-longline effort; similarly the cost of other options is high for this sector. Even with the status quo arrangements, the costs for auto-longline are high. Option 2 was implemented with some modification in 2013, extending the research zone further south to provide geographic continuity to the existing Commonwealth marine reserve (Figure 4.1).

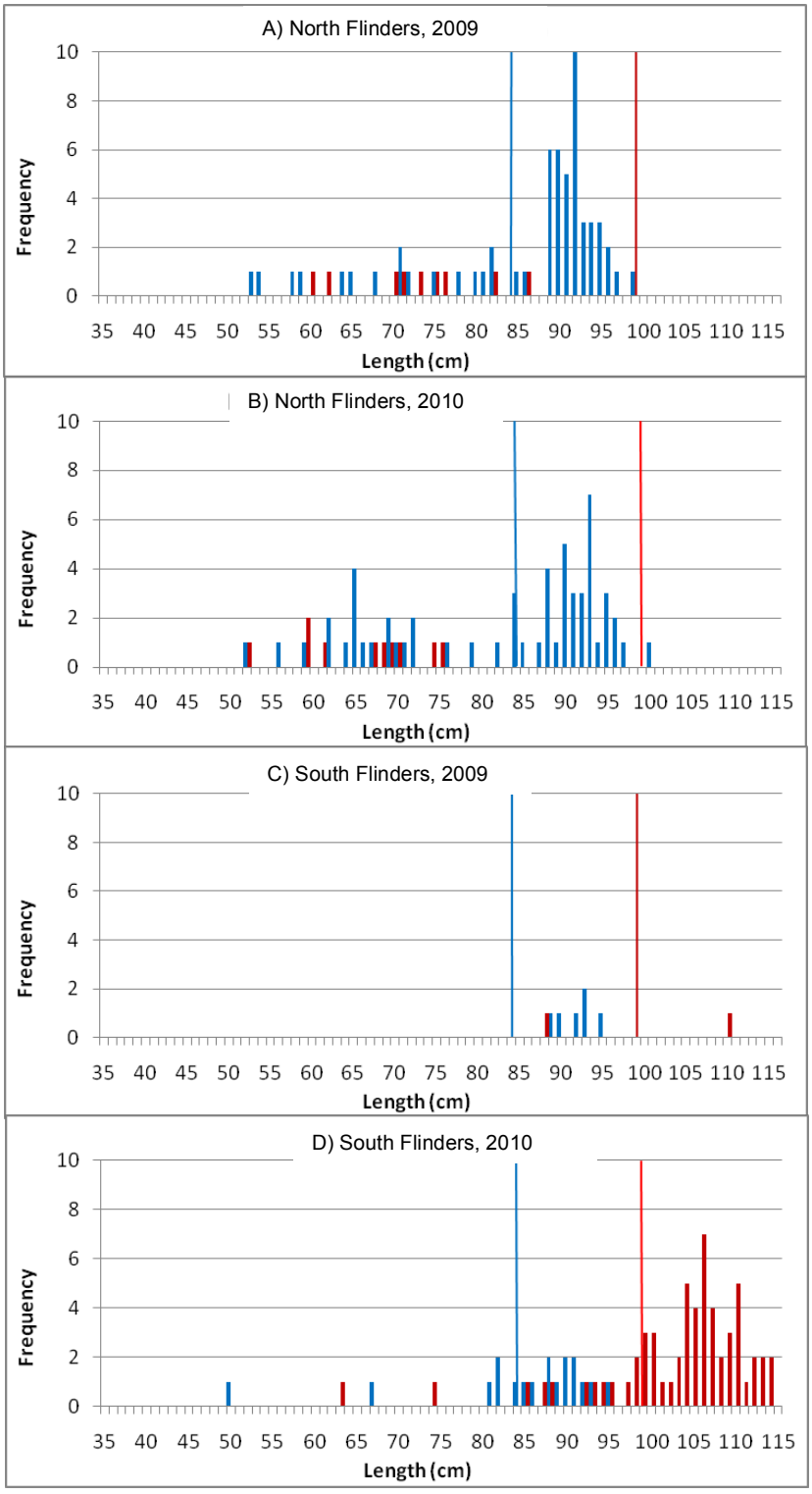


Figure 4.4 Length frequency of male (blue) and female (red) *Centrophorus harrissoni* at the Flinders Island area (Figure 4.1 A, D). Vertical lines indicate size at maturity.

Centrophorus harrissoni has been recorded in a series of patchy locations along the east coast of northern New South Wales (Figure 4.1A, F). Developing options for this region was difficult because survey data found demographic components of the population (males, females and juveniles), or at least where they were sampled, were widely separated, by >150 km in some cases. Any large closures would have major costs for the trawl industry, as large sections of the New South Wales continental margin coast are trawled. The Hunter reserve area is described here as an example of these challenges. Three options were developed: option 1 consists of a proposed Commonwealth marine reserve. Option 2 would extend the proposed reserve across the slope to cover the full depth range of *C. harrissoni.* Option 3 would extend the proposed reserve both along the slope to the south and across the slope. Only option 3 scored medium or high for all six conservation criteria; options 1 and 2 performed poorly in this regard because although mature females were recorded in the area, males and juveniles were rare (Figure 4.5 A) Confidence in the Hunter area to support recovery of *C. harrissoni* depends on extending the area to Port Stephens, a sampled location to the south where a substantial population of juveniles has been recorded (Figure 4.5B). This suggests its potential as a nursery area.

Potential trade-offs for trawl at the Hunter area could not be evaluated because of lack of spatial resolution in fisheries catch data collected under New South Wales (State) jurisdiction. None of the options were implemented because the trade-offs (costs to the fishing industry) were considered unacceptable by the New South Wales state jurisdiction. Instead the responsible agency relies on a total allowable catch of zero for all *Centrophorus.*

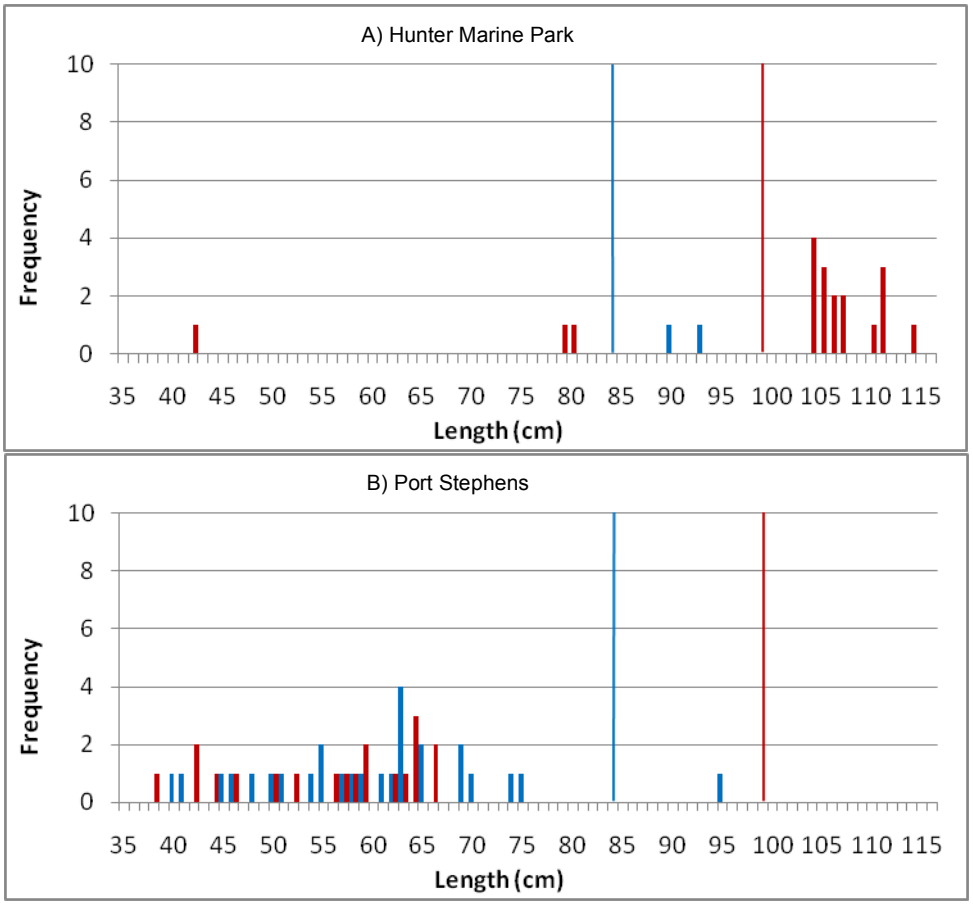


Figure 4.5 Length frequency of male (blue) and female (red) *Centrophorus harrissoni* at the Hunter area, New South Wales (Figure 4.1 A, F). Vertical lines indicate size at maturity.

Two options were developed for remote seamounts (Figure 4.1A): Option 1: Two seamounts closed - Taupo and Barcoo; Option 2: five seamounts closed with the addition of Queensland, Britannia and Derwent Hunter seamounts. Importantly neither option scored high for breeding success, which is uncertain because demographic data for these remote areas are limited. Moving from option 1 to option 2 would provide two contrasts in criteria scores: abundance would increase from medium to high, because historical catch records show higher catch rates from the additional seamounts. This would also result in a potentially high cost in lost auto-longline catch. Option 1 was implemented initially but expanded to option 2 in 2013 with the modification that hand reel fishing remains permitted on one seamount, which also contributed to research on survivorship.

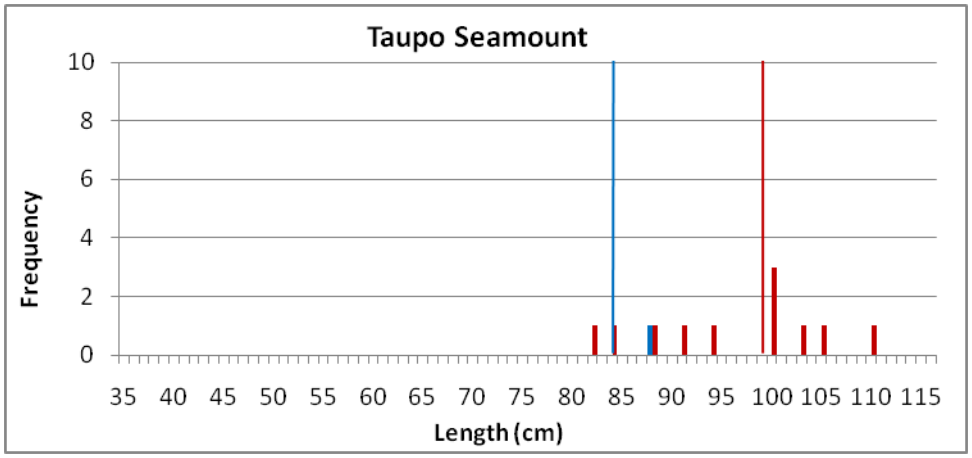


Figure 4.6 Length frequency of male (blue) and female (red) *Centrophorus harrissoni* at the Taupo Seamount (Figure 4.1 A). Vertical lines indicate size at maturity.

Stage 3: Evaluation of closures networks

The performance of the closures network for *C. zeehaani* was limited against the extent of occurrence and genetic diversity criteria because the western population could not be located (Table 4.3). Area of occupancy was increased in 2013 with the expansion of some area closures, improving the score to high. The trade-off was poorer performance against the economic criteria: higher lost trawl catch and more displaced trawl and auto-longline effort – all changing to high cost scores. In 2013 a fourth area was added – Murray (Figure 4.1A). The Murray area was initially not considered as an area option because it scored poorly at the screening stage. It was later added to the network because of modest cost to industry and it is adjacent to an existing Commonwealth marine reserve.

Table 4.3 Management strategy evaluation of closure networks for *Centrophorus* species.

Network and option	Conservation criteria			Economic criteria			
	7. Extent of Occurrence	8. Area of occupancy (km^2)	9. Genetic Diversity	10A. Lost trawl catch (t)	11A. Displaced trawl effort (operations/year)	10B. Lost auto-longline catch	11B. Displaced Auto-longline effort
C. zeehaani							
Coffin Bay + Sydney + Port MacDonnell	M+	M–H: (1869–3790)	L++	L–H: (>1.8–50.9)	M–H: (>36.2–355)	L	L –M
C. harrissoni							
Flinders + Seamounts	M	L–M: (1209–2903)	M	L: (7.2–7.4)	L: (97.6–98.2)	HH	HH
Flinders + Seamounts + Hunter	H	M–H (1596–3939)	H	M?: (>7.2–7.4)	M?: (>97.6–98.2)	HH	HH

Scoring: L= low. M= medium, H=High based on criteria and thresholds given in Table 1. t = metric tons. km = kilometres.

The performance of the current network for *C. harrissoni* against the conservation criteria was limited to medium scores by the exclusion of any areas off northern New South Wales (Figure 4.1A). Adding the Hunter area would increase all these scores to high. The trade-offs with resource use of adding the Hunter area were estimated to be a change from low to medium cost for trawl catch and displaced effort but this is uncertain due to lack of spatial resolution in catch data from New South Wales.

4.4 Discussion

This study explored options for marine spatial management of vulnerable *Centrophorus* sharks from Australia over three stages. The conservation objectives were to halt decline and support recovery of populations. The economic objectives were to limit lost catch and displaced effort. The results lay bare the trade-offs between these competing objectives.

Key areas for attention in the establishment and management of marine spatial management for biodiversity conservation and fisheries are information sharing, coordination and defining jurisdictions and stakeholders (Rice, Moksness *et al.* 2012). A key role of the scientist in the MSE process was to foster communication. This was both challenging and satisfying given the diverse group of stake-holders that held differing and opposing views on the value of the

resource use and conservation objectives. Forming the USDSWG exclusive of the stakeholders helped to focus the technical discussions on the species involved and develop the best possible conservation criteria given the uncertainties and assumptions. Stakeholders were then able to focus on their areas of knowledge and interest, by developing most of the options and participating in the evaluation.

Careful consideration of criteria for measuring performance against conservation objectives limited the trade-offs with resource use. Closing larger areas generally provides for greater carrying capacity and larger scope for recovery by dispersal over subsequent generations (Chittaro, Kaplan *et al.* 2010). A more immediate need for species like sharks that have internal fertilization and live young is maintaining breeding success, otherwise a population will decline to zero, even if there is no human induced mortality. In this respect the breeding success criterion can be effective for shark and ray species that are not highly dispersed if there are sufficient fishery or survey data on size distribution and sex ratios.

Patterns of sex and size-based segregation are evident in many deep-sea sharks including *Centrophorus*. Scientific authors for this group assume that the spatial scale of separation between males, females and juveniles represents the minimum geographic scale of a viable population that allows breeding and recruitment to occur without migration (Graham and Daley 2011; Moura, Jones *et al.* 2014). In this respect the breeding success criterion (2) was most important in Stage 2. Industry stakeholders from South Australia and Victoria who had collected additional survey data were able to identify smaller areas where breeding success could be achieved. They were in a better position to reduce trade-offs by identifying smaller closures that could provide for breeding success and limit the economic cost.

The economic criteria used in the MSE were value of lost catch and displaced effort. The quality of these data varied between state and federal sectors, particularly in terms of their spatial resolution. The federal (Commonwealth) trawl sector had the most detailed catch composition data for commercial species and the best spatial resolution for reporting (within 4 km^2). This sector was best able to argue in its own favour regarding the trade-offs in costs of lost production.

In Stage 1of the MSE, candidate areas were identified by stakeholders and short-listed using criteria 1–3. Identifying areas for data poor marine species can be difficult. Compared to the terrestrial environment, marine species are less likely to be linked to specific or even known areas. Identification of some candidate areas was informed by historical and new survey data and aided in part by the local knowledge of fishers (Williams, Althaus *et al.* 2013).

In Stage 2 options were developed and evaluated for the six areas that remained after screening. These options needed to be species-specific, because the geographic distributions of the two species only partly overlap. This makes the costs of lost economic production cumulative and certain to increase if more vulnerable species are managed by closures, an issue that has not escaped the notice of the fishing industry.

Area option development and selection was clearly influenced by the trade-offs, pointing to the value of providing a range of criteria covering the two key objectives. For most areas acceptable trade-offs could be identified. For the Flinders area in particular, large trade-offs were unavoidable. The research zone was initially implemented in this region to limit the direct trade-offs with cost of lost production but added complexity. This added complexity lead to increased implementation uncertainty, as well as increased costs of monitoring and compliance. The research zone was later closed.

Developing effective closure networks around the Australian continent was challenging because no overarching coordinating mechanism for reconciling the authority of the responsible agencies existed at the time. Financial costs of collecting survey data and co-ordination of the various meeting processes were more than $US 1/2 million This is a common challenge for ocean governance (Rice 2011). The sharks in this study were poorly known compared to more iconic species of birds and mammals (although better known than most bycatch fish species) adding to the costs. In this study, federal agencies responsible for fisheries and conservation had some success in aligning the fishery closures with national marine reserves. Co-ordination between the federal and state authorities responsible for fisheries and conservation was more challenging because the federal constitution in Australia was written before deep-sea resources were discovered and does not clearly allocate responsibility for their management.

Once established, effective management of closures and closure networks needs to be adaptive and include continued monitoring (Rice 2011). The strategies adopted in this case study were flexible enough to respond to a change in the species conservation plan from ‘halt decline’ to ‘support recovery’ by adding protected areas in 2013. This analysis also provided for better integration with Commonwealth marine reserves in 2013. There is still a need for ongoing monitoring of the closures for the species of concern, which will be challenging given the long timeframe for recovery of these low productivity species: 60+ years (Chapter 5). Monitoring of abundance, size structure and sex ratios is needed and would be aided by further research addressing key uncertainties including distribution, population structure and mobility. However most of these costs are attributed to (paid for by) the fishing industry, and

compete with priorities for monitoring target species and other aspects of the marine environment. Monitoring needs to be non-lethal, requiring additional (to commercial fishing) surveys, further adding to costs.

In conclusion, the loss of vulnerable data poor marine species is not inevitable but needs to be considered in light of the trade-offs with economic impacts on resource use that are high and cumulative as concerns are raised about more and more species. The Management Strategy Evaluation approach has been shown here to be a suitable decision support framework for exploring these trade-offs inherent in spatial management. The scientists involved in this study helped play a facilitating role by predicting the economic and ecological consequences of alternative courses of action against competing objectives in a manner that is, to the extent possible, accurate, reproducible, transparent, independent and policy neutral. The approach was also able to accommodate a range of scientific views that emerged when faced with uncertainties in data and knowledge. Where data were limited, semi-quantitative criteria were adopted successfully, and in some cases expert judgment was deployed. Appropriate selection of criteria can limit the trade-offs to some extent. Residual uncertainty means that once established, effective marine spatial management including closures for data poor vulnerable marine species requires ongoing monitoring and adaptive, flexible management. For long-lived species such as deep-sea sharks, this requires planning over decades.

CHAPTER 5. SIMULATION-BASED EVALUATION OF RESERVE NETWORK PERFORMANCE FOR A VULNERABLE MARINE SPECIES

5.0 Abstract

An individual-based simulation model of the reproduction and movements of *C. zeehaani* (IBM) was developed and applied to determine how long a depleted population would take to recover from its current status of 8% of un-fished numbers to a target of 20%. Individual movement patterns were based on tracking results and simulated across a spatial domain of three closures and fished areas with three different types of fishing gear and fishing restrictions. Key uncertainties were length of the female breeding cycle, natural mortality (*m*) rate and spatial variation in population density. The base case (three year breeding cycle, 2% *m* and survey based spatial variation in abundance) predicted recovery to 20% of pre-exploitation numbers in 63 ± 3 years. Poor matching of closure locations to population density would delay recovery by an additional 31.9 years. Sensitivity testing predicted that the target would be reached 19.2 years earlier with a 2-year cycle or 16.5 years later than the base case with a four-year cycle. If *m* were half the base case estimate then the target would be reached 13.5 years earlier or, significantly, if *m* were double the base case estimate, recovery to the target would take 98.3 years longer than the base case. Improving handling practices for sharks or changing fishing methods on the continental shelf would not significantly affect the time for recovery but re-introducing trawling for orange roughy (*Hoplostethus atlanticus*) in deep waters would delay recovery by an additional 45.9 years. Doubling the size of a closure where *C. zeehaani* are abundant would reduce recovery time by 9.9 years; halving closure size there would increase recovery time by 12.6 years. Such changes would have no significant effects where *C. zeehaani* were not abundant. The model can be used to evaluate the consequences of alternative management interventions and the risks associated with key uncertainties and can be applied to other shark species with telemetry data.

5.1 Introduction

The deep-sea (> 200 m) is the world's largest ecosystem, with more than 90% of the inhabited volume of the planet, and has high biodiversity (Clarke, Milligan *et al.* 2015; Mora, Tittensor *et al.* 2011). This region is also vulnerable to a range of anthropogenic activities, including deep-sea mining, fishing and pollution (Koslow, Boehlert *et al.* 2000; Levin and Bris 2015; Schlining, S. von Thun *et al.* 2013). Many deep-sea species, particularly sharks and rays, are vulnerable to these anthropogenic activities because of slow growth, late maturity and low fecundity (Kyne and Simpfendorfer 2010; Last and Stevens 2009; Rigby and Simpfendorfer 2015). In addition to issues with observing deep-sea species, conserving and managing these species is challenging because movement ecology and mobility of most populations are poorly known (Daley, Williams *et al.* 2015) (Chapter 3).

The most taxonomically diverse deep-sea shark group is the Squaliformes comprised of five families with many endemic species (Kyne and Simpfendorfer 2010; Last and Stevens 2009) (Chapter 1). Of particular concern are the gulper sharks (*Centrophorus*, Centrophoridae) a group of medium sized (0.7–1.7 m) sharks from the continental slope of the world's oceans (Compagno, Dando *et al.* 2005; Daley, Appleyard *et al.* 2012; Verissimo, Cotton *et al.* 2014) (Chapter 2). This group exemplifies low productivity species adapted to the stable deep-sea environment (Daley, Williams *et al.* 2015) (Chapter 3). Young are born live in small litters of only 1 or 2 pups after a long gestation of up to 3 years in some species (Graham and Daley 2011; McLaughlin and Morrissey 2005). Females of some *Centrophorus* species do not mature until 17–24 years of age (Whiteley 2008).

Fishing has depleted at least six species of *Centrophorus* in the northeast Atlantic, southwest Pacific and Indian Oceans (Adam, Merrett *et al.* 1998; Graham and Daley 2011; ICES 2010). Zero catch limits have effectively ended targeted fishing for *Centrophorus* in the northeast Atlantic and off south-eastern Australia but these species remain vulnerable even as bycatch in multi-species fisheries because sustainable yield levels are less than 5% of un-fished biomass (AFMA 2012; Forrest and Walters 2009; ICES 2005). Given this extreme vulnerability, complete protection, in the form of fishery closures appears to be the only plausible solution to conserve populations of *Centrophorus* that have been previously been heavily targeted and depleted (Daley, Williams *et al.* 2015) (Chapter 3).

The most detailed and comprehensive management strategy in response to overfishing of *Centrophorus* has been implemented off southern Australia for two species: *C. harrissoni* and *C. zeehaani* (AFMA 2012) (Chapter 4). In this region, these species are restricted to temperate waters of southern Australia and nearby seamounts (Last and Stevens 2009; White,

Ebert *et al.* 2008). Declines of more than 90% in key parts of their range have lead to national protection for both species. Central to the management strategy is a network of areas closed to all fishing methods specifically for protection of *C. zeehaani and C. harrissoni* (AFMA 2012) (Figure 5.1) (Chapter 4). The strategy also includes other measures including a zero total allowable catch for *Centrophorus* and a code of practice for releasing any *Centrophorus* caught incidentally. Australia also has a network of Commonwealth marine reserves implemented to conserve marine biodiversity generally that has some potential to contribute to the recovery of *Centrophorus* populations (Environment 2015).

Closed areas are used widely to conserve marine biodiversity and manage the impacts of fisheries on vulnerable species including sharks and rays (Bonfil 1999; Sobel 1993; Sumaila, Guénette *et al.* 2000). Closure location, size and spacing are critical attributes for effective closure network design and for integration with other management measures (e.g. catch limits, closed seasons and gear restrictions) (Chittaro, Kaplan *et al.* 2010; Ruijs and Janmaat 2005) (Chapter 4). Understanding home range and movements of individuals and populations is key to informing these attributes (Babcock, Egli *et al.* 2012; Daley, Williams *et al.* 2015) (Chapter 3).

Passive acoustic telemetry is an established electronic tagging method used for studying home range and movements of sharks and to inform the design of closures for managing populations (Andrews and Quinn 2012; Heupel, Semmens *et al.* 2006). Keys steps in the method are fixing transmitter tags to the sharks and deploying an array of receivers to detect transmitters as they move into proximity (Heupel, Simpfendorfer *et al.* 2004; Knip, Heupel *et al.* 2012). Receivers are attached to moorings that are recovered periodically (generally after 6–24 months) to download data for analysis. This method has some key advantages for deep-sea tracking in that the data can be collected remotely without having to recapture the tag. A disadvantage is that the scale of data coverage can be limited by logistical challenges of deploying large receiver arrays in the deep ocean (Daley, Williams *et al.* 2015) (Chapter 3).

Passive acoustic telemetry has been used to study the movements of 71 individual *C. zeehaani* off southern Australia; the only comprehensive study of its kind for deep-sea sharks from the upper-continental slope (Daley, Williams *et al.* 2015) (Chapter 3). Data were collected off south Australia within the boundaries of the Coffin Bay Closure, the largest of the Australian closures implemented for *Centrophorus* (Figure 5.1) (Daley, Williams *et al.* 2015) (Chapter 3). Models based on these data were developed to describe movements over intermediate closure scales (tens of km's), providing input into decision-making regarding closure size. Catch and effort surveys have identified areas where mature males and females

and juveniles occur together at relatively high abundance. These areas of higher density have been used as proxies for identifying mating and breeding areas to also inform location of closures (Chapter 4). An important limitation of the telemetry data was that receivers could not be deployed on the seafloor between closure areas (because of high risk that the moorings would have been tangled in fishing gear). To date, this has limited the ability of telemetry approaches to inform spatial management decisions over larger scales (>1000 km).

Simulation models are an alternative approach to assess the efficacy of marine reserves in mitigating the effects of fishing on populations (Attwood and Bennett 1994; Gerber, Botsford *et al.* 2003). The key advantage of simulation is that many scenarios can be evaluated quickly. Key uncertainties often include individual mobility and models are particularly sensitive to movement of fish across reserve boundaries (Gerber, Botsford *et al.* 2003). For many fish species movement data is available at the spatial scale of a single closure but there is usually limited data across the range of a population, particularly in the deep sea because it is logistically problematic (Daley, Williams *et al.* 2015; Gerber, Kareiva *et al.* 2002; Kramer and Chapman 1999) (Chapter 3). Thus, integration of observations over a smaller scale and modeling approaches over a larger scale is essential. The effectiveness of reserves is affected by individual variation in movement, which is significant in *C. zeehaani* (Daley, Williams *et al.* 2015; White, Botsford *et al.* 2011) (Chapter 3) therefore modeling approaches need to account for this variation (Babcock, Egli *et al.* 2012). The modeling approach also needs to be applied at appropriate spatial and temporal scales. Most studies to date have looked at responses over a few years in one or a few reserves. There are only a few examples where small networks of closures have been studied (Babcock, Egli *et al.* 2012; White, Botsford *et al.* 2011). The network of closures for *C. zeehaani* in southern Australia extend across thousands of kilometers and the recovery plan is predicted to take decades (Daley, Williams *et al.* 2015) (Chapter 3). To date there have been no simulation modeling studies of the effectiveness of closure networks across such large spatial and temporal scales.

Here we develop an individual-based movement model for extrapolating local scale movement data across regional scales, using *C. zeehaani* as the case study species. The model simulates structure of a population across the spatial scale of the network for generations. The model is conditioned with detailed passive acoustic telemetry data collected from the largest *Centrophorus* closure (Figure 5.1) and with biological parameters from the literature. A number of scientific uncertainties, including natural mortality and fecundity, were explored using sensitivity tests. A range of management scenarios was explored including improving handling survivorship, increasing closures, or changing fishing effort – in terms of amount, type of gear, or size of footprint. We show how this simulation approach can be applied to

assess population recovery over several generations across a geographic range that includes multiple areas closed to fishing.

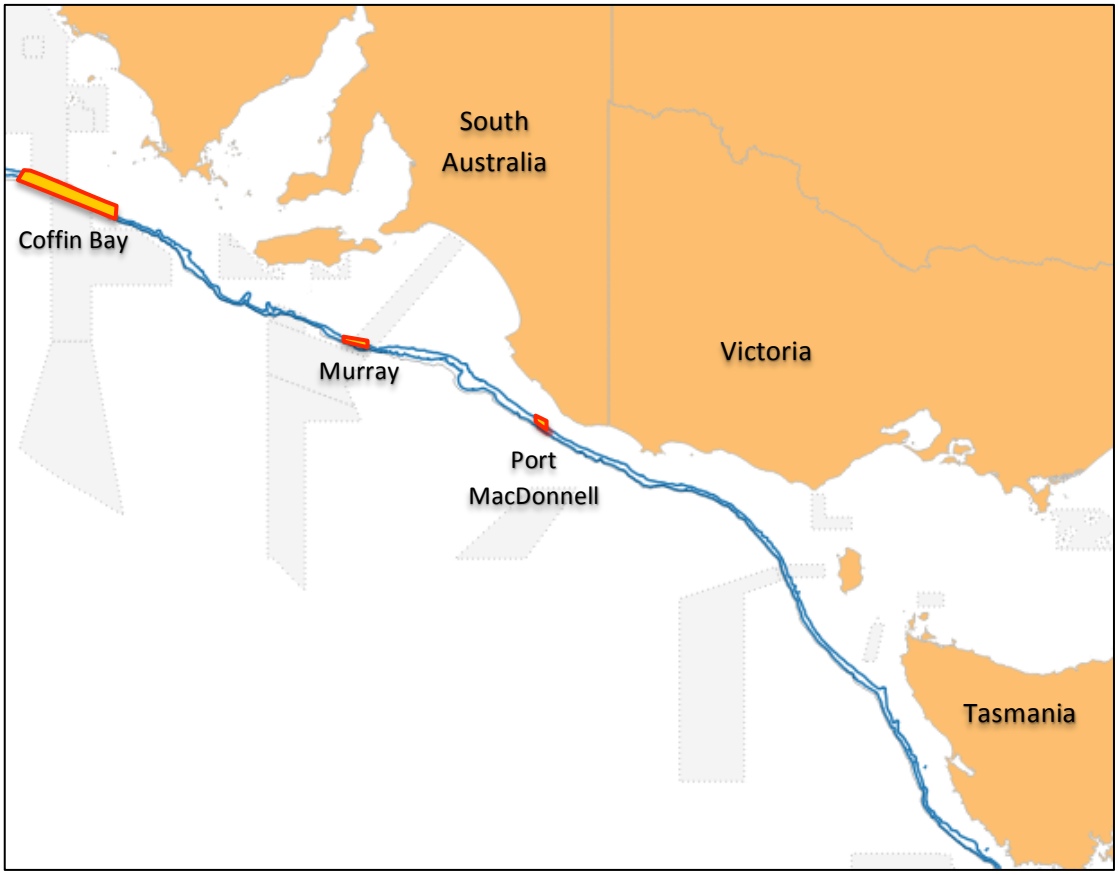


Figure 5.1: Geographic domain of *Centrophorus zeehaani* central population off southern Australia. Blue lines indicate the bathymetric range of *C. zeehaani:* 220–850 m, red boxes indicates closures, grey boxes indicates marine parks.

5.2 Methods

We developed an individual-based, size-specific modeling approach to assess whether a model population of *C. zeehaani* could recover from depletion within its range off southern Australia (Figure 5.1). The model domain consisted of fished and un-fished areas. Individual movements were based on passive acoustic tracking data for *C. zeehaani* over a 15 month period (Daley, Williams *et al.* 2015) (Chapter 3). A series of trials/runs explored performance under present fishing conditions and several alternative scenarios. Factors such as fecundity, natural mortality (m), fishing mortality (f) and size at birth were based on the literature (Table 5.1) or else calculated as described below. Natural mortality, f, individual growth and births were attributed to the population instantaneously at the end of each year. Performance was defined as the lowest possible number of years for the model population to increase 2.5-fold to reflect recovery from the central populations current depleted state of 8% of initial

numbers (Williams, Althaus *et al.* 2013) to a target of 20%. A target of 20% was chosen to be consistent with limit reference points for wild harvest fisheries in Australia (Patterson, Georgeson *et al.* 2015). Each trial was replicated ten times (Figure 5.3).

Model domain

The geographic domain for the simulation was the putative geographic range of the southern population of *C. zeehaani* along the upper-continental slope from off Ceduna (South Australia) to South West Cape (Tasmania). The gently sloping Ceduna Terrace to the west of the population and the shallow waters between Victoria and Tasmania are considered barriers to dispersal based on survey data (Section 4.2). The range included three fishery closures: Coffin Bay, Murray and Port MacDonnell. The Coffin Bay and Murray closures overlap with Commonwealth marine parks (Figure 5.1).

The model domain was based on the geographic domain and scaled in two dimensions (i) along the continental slope (longitude) and (ii) across the continental slope (deeper-shallower seafloor). The along-slope dimension was bounded at 0 km at the western boundary of the population and 1,888 km at the eastern boundary. The across-slope domain was scaled by the published bathymetric depth range of *C. zeehaani* (rather than latitude) and limited shoreward by the 220 m contour and seaward by the 850 m contour (Daley, Williams *et al.* 2015; Graham and Daley 2011) (Chapter 3). The domain was represented in the model as a simplified rectangular design, (Figure 5.2). Movements were simulated on an hourly time scale.

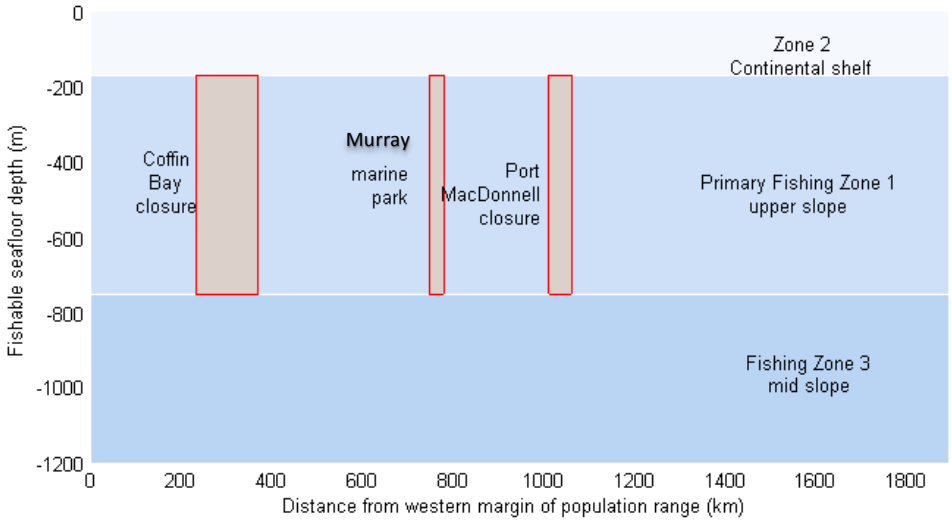


Figure 5.2 Two-dimensional model domain of fishing zones and closures within the geographic range of the central population of *Centrophorus zeehaani* off southern Australia.

Starting population

A virtual population was created at the start of each replicate run. Sex was allocated to individuals at random, assuming a ratio of 1:1. Size was allocated based on survey length frequency data obtained from Portland, Victoria in 2000–02 (Graham and Daley 2011). This dataset was chosen from among several candidates because it was the earliest and most likely to be similar to the un-fished population. Female maturity was determined by comparing the length of each individual at the end of each year to the published length at maturity: 960 mm (Graham and Daley 2011). It was assumed that females would always find mature males for breeding. Female *C. zeehaani* are thought to have a three year breeding cycle based on size classes of the embryos of a related species, although this is not entirely certain (McLaughlin and Morrissey 2005) (Chapter 3). In the base case each mature female had a cycle stage of 1–3, initially allocated at random.

For most scenarios, along-slope starting positions were allocated using a quarter degree (of longitude) linear grid. The allocations were drawn at random from a distribution of relative abundance generated from two existing sources: preferably catch and effort (rate) data from surveys in 2005 and 2009 (Williams, Daley *et al.* 2012) or alternatively, for grid intervals where catch and effort data were not available, from published estimates based on fishing effort and carrying capacity (Williams, Althaus *et al.* 2013). The two sources were calibrated against each other using data from the Coffin Bay closure where both types of measurements

have been reported previously. The only exception was a sensitivity test that used a random geographic distribution assuming a continuous uniform distribution. In all scenarios, across-slope positions were allocated at random from the range 220–850 m seafloor depth, assuming a continuous uniform distribution.

Table 5.1 Parameters used in the base case model and sensitivity tests using minimum and maximum values for *Centrophorus zeehaani* and its fisheries

Parameter	Base case	Min	Max	Source
Litter Size	1 pup			(Graham and Daley 2011)
Size at birth	41.5 cm			As above
Female size at maturity	95.7 cm			As above
Female age at maturity	29 years			(Whiteley 2008)
Female maximum age	35 years			As above
Female cycle	3 years	2	4	(McLaughlin and Morrissey 2005)
Natural mortality	0.02	0.01	0.04	(Daley, Williams *et al.* 2015; Hamlett and Koob 1999; Hernández, Daley *et al.* 2015) (Chapter 3)
Female dispersal factor	1E-5			(Daley, Williams *et al.* 2015) (Chapter 3)
Male dispersal factor	0.70			As above
Minimum depth	220 m			(Graham and Daley 2011)
Maximum depth	850 m			(Daley, Williams *et al.* 2015) (Chapter 3)
Fishing mortality	0.26	0.20	0.26	(Zhou, Smith *et al.* 2007)
Fishable depth		0	1200	(Daley, Last *et al.* 1997)

Further details of the fishing mortality values used are given in Table 5.2.

Individual movements

Simulated movements were based on data from an empirical acoustic telemetry study (Daley, Williams *et al.* 2015) (Chapter 3). All sharks were tagged with acoustic transmitters that had been fitted with depth and temperature sensors. Individuals were then tracked by an array of receivers deployed inside the Coffin Bay Closure. The array consisted of receivers arranged in five curtains across the slope. Curtains were arranged along the slope some 17–24 km apart. Details of the capture, tagging and tracking procedures and the results of the tracking are given in Chapter 4.3. No fish were tracked outside the Coffin Bay closure and we assumed the general pattern of movement outside the closure was similar to the pattern inside.

A distribution of average hourly movements along the slope was generated from observations of movements between receiver curtains (Figure 3.1) (Daley, Williams *et al.* 2015) (Chapter 3). These data were then filtered to remove movements between non-adjacent curtains (Figure 3.1). This eliminated movements where an individual may have left the array for an unknown period (passed a curtain without detection), which would be impossible to standardize for time. Movement distances between the curtains were then divided by number of hours between observations to obtain the average distance moved in an hour. To simulate daily

movements along the slope an hourly movement was chosen from the distribution at random at the start of each 24-hour period then repeated 23 times in the same direction.

A series of steps were taken to check data quality and ensure that predation or attacks on *C. zeehaani* by larger sharks had not affected the hourly movements. Any movement faster than 2 km/hr. was considered unlikely for *C. zeehaani*, potentially attributable to a White Shark (*Carcharodon carcharias*) or Shortfin Mako (*Isurus oxyrinchus*). The depth data were used to check for unusual diving patterns for all tags fitted to *C. zeehaani* that showed movements faster than 2 km/hr. (Appendix II). Where unusual depth patterns were found, the temperature data were also checked for elevated temperatures (body warmer than surrounding water). The movement data had already been filtered to check for single detections that could be potentially provide spurious high movement rates (Chapter 3).

Along-slope movements were modified to account for homing behavior. The published telemetry study found tagged female *C. zeehaani* tended to remain resident inside the Coffin Bay closure whereas males did not (Daley, Williams *et al.* 2015) (Chapter 3). After 15 months that study found the number of males detected in a given month had fallen by 31% but the number of females had fallen by only 6.8%. To replicate this sex-based difference a 'homing/dispersal factor' was incorporated into the hourly movements along the slope (Table 5.1). When an hourly movement away from the starting location was selected for an individual shark, it was reduced using the homing factor. Movements towards starting locations were not reduced. Homing factors were tuned by simulation testing to match the falls in detection rate described above for females and males. For this testing the model domain was constrained to be 124 km wide (along-slope) (equivalent to the Coffin Bay Closure). For the remaining simulations, along-slope movements were constrained to the geographic domain of the population. For any shark that was outside the domain at the end of a given day, an arbitrary movement of 1 km towards the center of the domain was added.

Hourly movement across-slope was simulated using deterministic and stochastic components. Initial across-slope position for each individual was selected at random from within the known bathymetric range of 220–850 m. The deterministic component was an hourly movement that approximates an observed diurnal movement towards shallow waters at night and deep waters during the day (Daley, Williams *et al.* 2015) (Chapter 3). This movement was represented by the following formula that has been simplified (to exclude effects of season, moon and seafloor habitat):

$$1/24 \times (\sin((hr-6)/4)) \times 100)$$

Each hour, each individuals across-slope position was modified by this deterministic component. Its position was then checked to see if it was still between 220–850 m. For individuals within this range, a stochastic component is selected at random from within the range -10 to + 10 m and the position modified accordingly. For individuals that have moved outside this known bathymetric range the stochastic component was replaced by a fixed value of -20 m (for individuals that are too shallow) or + 20 m (if too deep).

The model was simulated using Matlab software.

Annual mortality

Natural mortality (*m*) and then fishing mortality (*f*) were applied to the population instantaneously at the end of each model year. Natural mortality was calculated as 0.42 *k,* (*k*=growth parameter of the von Bertalanffy growth model 1938) based on an average value of *k* calculated from 30 elasmobranch species (Frisk, Miller *et al.* 2001). As there are no published values of *k* for *C. zeehaani* or *C. harrissoni,* we used a published value for *Deania calcea* (Centrophoridae) from Australia: *k* = 0.49 (Irvine, Daley *et al.* 2012). Therefore $m=0.4 \times 0.49 = 0.020$.

Different *f* rates were applied to individuals outside closures in each of the three different bathymetric depth zones. The zones were based on the different fishing methods permitted by regulations that were already restricted to manage commercial species (Table 5.2). For the base case, we used regulations in place when closures were implemented (Wilson, Patterson *et al.* 2009): Fishing Zone 1, upper-slope waters between the 173–750 m bathymetric contours. Trawling and auto-longline fishing were permitted, but gillnetting was excluded to protect school sharks, *Galeorhinus galeus*. Fishing Zone 2, continental shelf waters inshore of the 173 m bathymetric. Gillnetting and trawling were permitted but auto-longline fishing was excluded to limit unintended catches of Gummy Shark, *Mustelus antarcticus*. Fishing Zone 3: mid-continental slope waters offshore and deeper than the 750 m bathymetric contour where all fishing was excluded to protect Orange Roughy, *Hoplostethus atlanticus*. Instantaneous *f* values for these fishing methods were obtained for *C. zeehaani* from published risk assessments (Zhou, Smith *et al.* 2007) (Table 5.2). In the model, individual sharks were removed from the population in each zone in proportion to the summed *f* for the different fishing gears permitted. The individuals removed were selected at random.

Table 5.2 Model domain fishing zones with different fishing methods and associated fishing mortality for the permitted methods.

Zone	Minimum seafloor depth	Maximum seafloor depth	Permitted methods	Prohibited methods	Fishing mortality
2. Continental shelf	0	176	gillnet, trawl	auto-line	0.09 + 0.11
1. Upper-Continental slope fished	177	750	auto-line, trawl	gillnet,	0.15 + 0.11
3. Upper-Continental slope closed	177	750	Nil	All	0.00
4. Mid-continental slope	751	2000	auto-line	gillnet, trawl	0.00

Annual individual growth

Female *C. zeehaani* take 29 years to grow from 41.5 cm at birth to 95.7 cm at maturity (Last and Stevens 2009; Whiteley 2008) an average of 1.87 cm/year. This annual growth was added to the size of each modeled individual at the end of each year. Females that grew larger than the size at maturity at this time were re-classified as mature. For each mature female, the cycle stage was incremented by one year. At the end of the breeding year of the cycle (stage 3 in a 3 year cycle), the stage was reset to 1.

Annual population growth

After accounting for annual mortality, mature females reproduced. At the end of every year, a single pup was added to the population for every mature female in the third year of the breeding cycle. The size at birth for each pup was set at 41.5 cm based on the average of published values (Table 5.1). Sex was assigned at random to the new pups. The starting location for each pup was matched to the co-ordinates of the mother at the end of the birthing year.

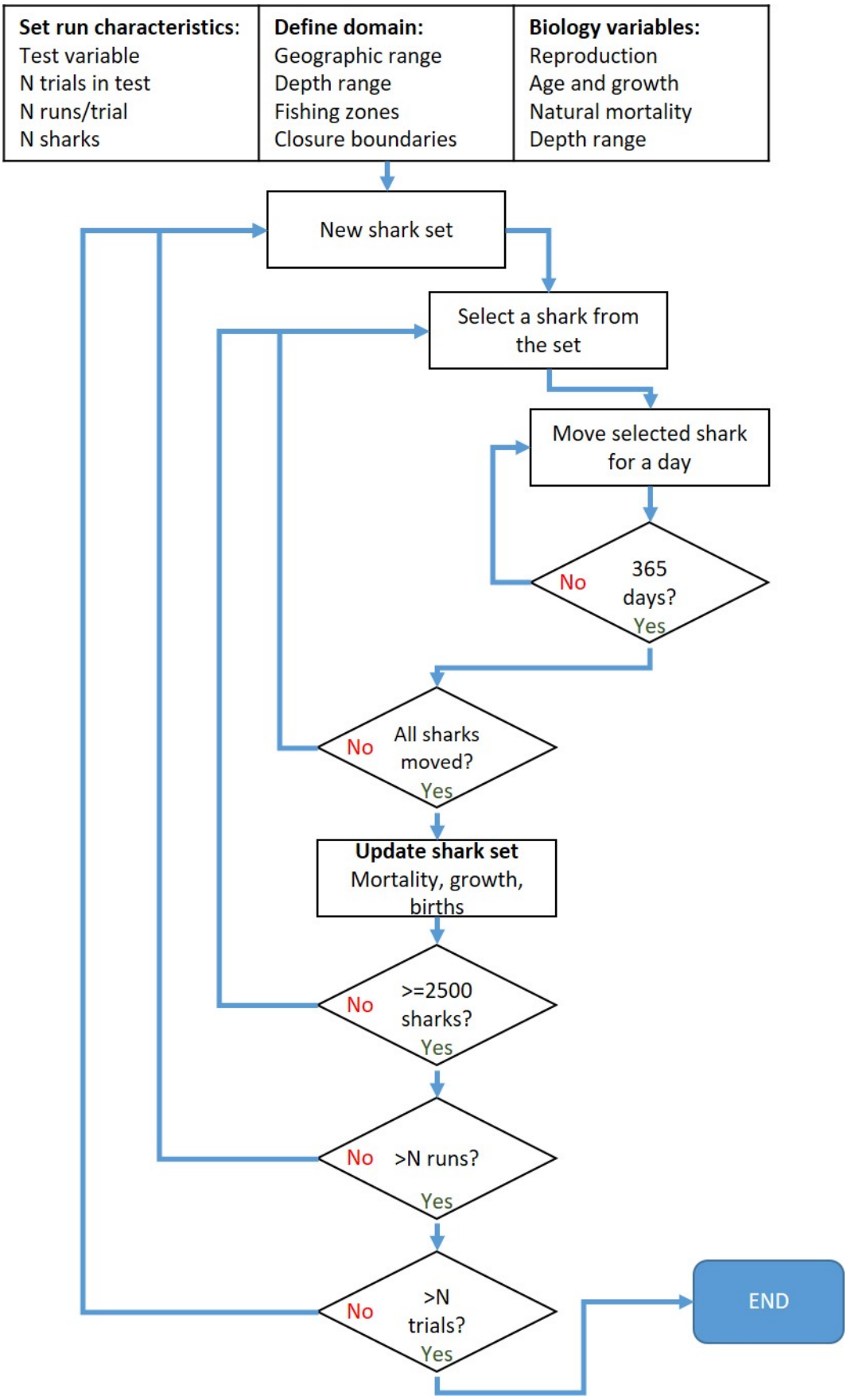


Figure 5.3 Simulation model outline showing starting inputs, processes and outputs

Scenario evaluation.

Two groups of scenarios were tested to explore how the shark population would respond to changes, firstly to permitted fishing methods, and secondly to closure size. Fishing method scenarios included: Stopping gillnetting and introducing auto-longline fishing on the continental shelf, as proposed to reduce sea-lion mortality; Reintroduction of trawling for orange roughy in waters deeper than 750 m; Improving handling practices in the auto-longline sector such that more sharks were released alive (handled in the model by halving the fishing mortality due to auto-longline). Closure scenarios included doubling or halving the size of closures located where *C. zeehaani* were abundant or, alternatively, not abundant.

Summarizing the model results

The primary output of the model is the number of the years it takes the population to increase from 8% of initial biomass to 20% of initial biomass. This is represented in the model as an increase from 1000 individual sharks to 2500. The base case, sensitivity tests and scenarios were repeated 10 times each. The number of years to recovery is represented as the average for the 10 replicate runs and variation is represented by the standard deviation.

5.3 Results

Starting population

The length frequency input data consisted of a large proportion of juvenile males and females, a large proportion of adult males, and a relatively small proportion of adult breeding females (Figure 5.4).

Analysis of survey catch and effort data and carrying capacity estimates found along-slope distribution of the population was concentrated in two areas (Figure 5.5). The first concentration covered a wide area from 220–540 km east of the western margin of the population range; approximately half of which was contained by the Coffin Bay closure towards the west of the range. A second concentration formed a narrow peak at 1000–1040 km and was fully enclosed by the Port MacDonnell closure. Lower background abundance extended across the remainder of the range, becoming patchy towards the eastern margin. The Murray closure was located over an area of low abundance.

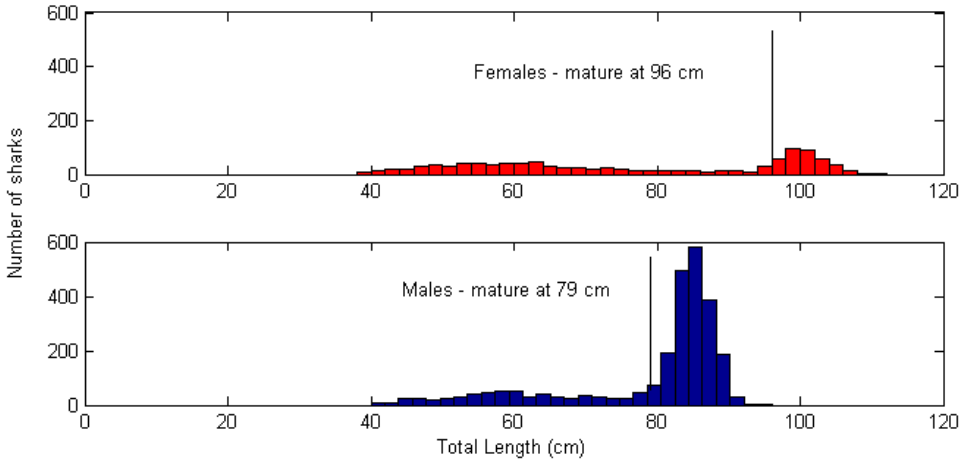


Figure 5.4 Input length frequency distribution of *Centrophorus zeehaani* population off Southern Australia.

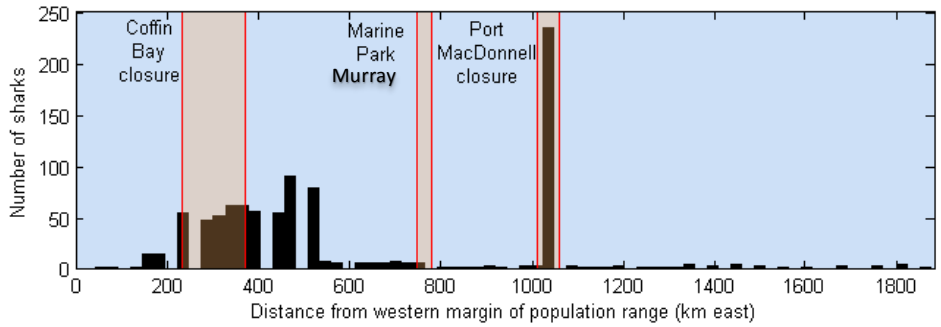


Figure 5.5 Input along-slope geographic distribution of a *Centrophorus zeehaani* population

Individual movements

Analysis of the passive acoustic tracking data found most movements were slow (Figure 5.6). For females 99.6% of the 1888 hourly observations were slower than 1 km/hr. and there were no observations of > 2 km/hr. For males 99.5% of the 18103 hourly observations were slower than 1 km/hr. and only 0.1% of observations, 21 in total, were faster than 2 km/hr. These 21 unexpectedly fast observations represented 13 individuals. The individual longitude and depth plots were examined for unusual patterns of behaviour (Appendix II). Of these, only one individual with tag number 779 showed unexpectedly shallow ascents. The temperature record of 779 showed a range of 7–12 degrees centigrade, which is consistent with the surrounding environment. Given that there was no clear evidence of predation and that the number of faster than expected observations (> 2km/hr.) was extremely low, the full set of observations were used for the base case.

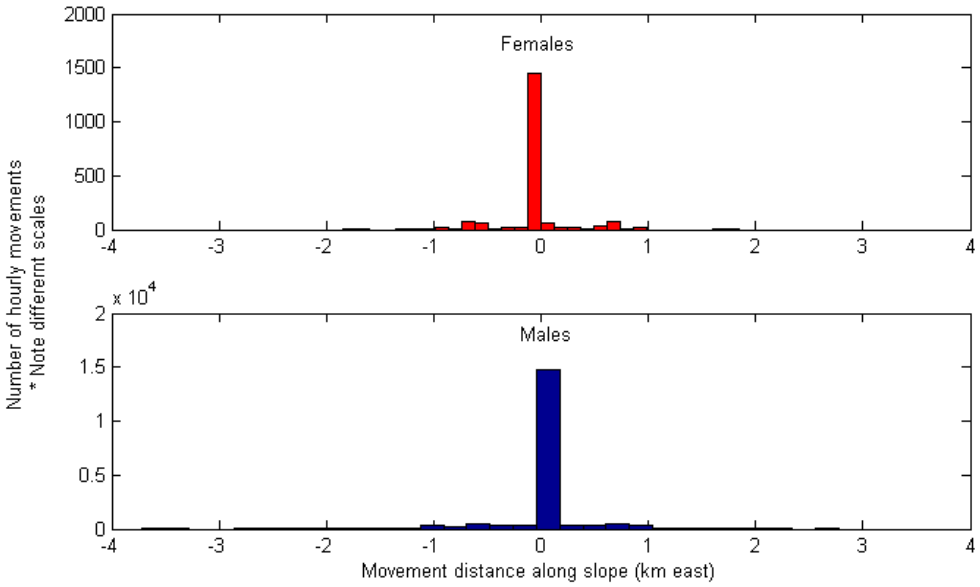


Figure 5.6 Input frequencies of hourly along-slope movement distances by individual *Centrophorus zeehaani* off southern Australia

Base case estimate of recovery time

The base case simulation (three year female cycle, m=0.02, population density based on survey data) showed population trends in space (Figure 5.7) and time (Figure 5.8). In the first ten years the population declined from 1000 to 600. Surviving individuals remained close to their release points in two concentrations: 1 in the Coffin Bay closure and fished area immediately to the east, 2 in the Port MacDonnell closure. Sharks were distributed across the remaining fished areas in low abundance (Figure 5.8). There were few sharks within the Murray closure at any stage of the simulation because the initial numbers seeded there were low. Individual locations started to show a distinct clumping pattern. This corresponded to the start locations of females that were seeded into the domain at 0.25 degree intervals and were tightly constrained in their along-slope movements by the homing factor.

After 50 years the population increased to around 1,500 sharks (Figure 5.7c) and the rate of population increase had also steepened somewhat (Figure 5.8). The modeled population continued to contract along-slope and became highly concentrated within the Coffin Bay and Port MacDonnell closures. Overall the base case predicted the starting population of 1000 would take 63.1 ± 3.1 years to increase to 2500 (Table 5.3).

Sensitivity tests

The model predictions were not sensitive to the 21 unexplained observations of movement rates > 2km/hr. (Test 1A, Table 5.3). When these were removed from the base case the model predicted recovery in 64.3±2.5 years, which was not significantly longer than the base

case. The model predictions were sensitive to: 1 length of female reproductive cycle, 2 natural mortality and 3 patchiness in along-slope distribution. If the female cycle was only two years then predictions were optimistic, with recovery achieved in 43.9 ±1.4 years (Table 5.3) (Figure 5.8), 19.2 years faster than in the base case (3 year cycle). Conversely predictions were pessimistic with a four-year cycle, recovery would take 79.6±3.6 years, 16.5 years longer than the base case. With m=0.01 (half the base case estimate) recovery would take 49.6 ±1.3 years, 13.5 years longer than the base case prediction. Importantly if m was double the base case estimate then recovery would take161.4±10.6 years, 98.3 years longer than the base case prediction. The base case considered that the along-slope distribution of *C. zeehaani* is patchy (Figure 5.5). If instead this distribution were uniform, then recovery would take 94.9±5.8 years, 31.8 years longer than the base case predicted.

Table 5.3 Summary of results showing time taken for population to recover to 2500 animals including sensitivity tests and scenario analyses

Trial	F1 upper-slope	F2: shelf	F3 mid-slope	Average (years)	SD	Performance consequence (D years)
1. Base case	0.260	0.200	0.000	63.1	3.1	0
Sensitivity tests						
1A. Base case + speed < 2 km/hr.	‘’	‘’	‘’	64.3	2.5	1.2
2. Short cycle (2 years)	‘’	‘’	‘’	43.9	1.4	19.2
3. Long cycle (4 years)	‘’	‘’	‘’	79.6	3.6	-16.5
4. Low mortality (0.01)	‘’	‘’	‘’	49.6	1.3	13.5
5. High mortality (0.04)	‘’	‘’	‘’	161.4	10.6	-98.3
6. Uniform geographic distribution	‘’	‘’	‘’	94.9	5.8	-31.8
Observed geographic distribution*	‘’	‘’	‘’	63.1	3.1	0
Fishing scenarios (M= 0.02, females cycle = 3, distribution =observed)						
7. Change gillnetting to auto-longline	0.260	0.260	0.000	63.9	2.1	-0.8
8. Allow orange roughy fishing	0.260	0.200	0.110	109.0	4.9	-45.9
9. Improve handling practices	0.185	0.200	0.000	62.7	2.7	0.4
Closure scenarios (M= 0.02, females cycle = 3, distribution =observed)						
10. Double the size Coffin Bay closure	0.260	0.200	0.000	50.6	2.0	12.5
11. Halve size Coffin Bay closure	‘’	‘’	‘’	75.1	2.7	-12.0
12. Double size of Murray closure				63.4	2.5	-0.3
13. Halve the size of Murray	‘’	‘’	‘’	63.8	1.5	-0.7

All trials used 1000 individuals for 10 replicates, male dispersal = 0.7, female dispersal=1e-5. SD= standard deviation, F = fishing mortality for a given zone. The base case uses observed geographic distribution and is repeated for comparison with trial 6.

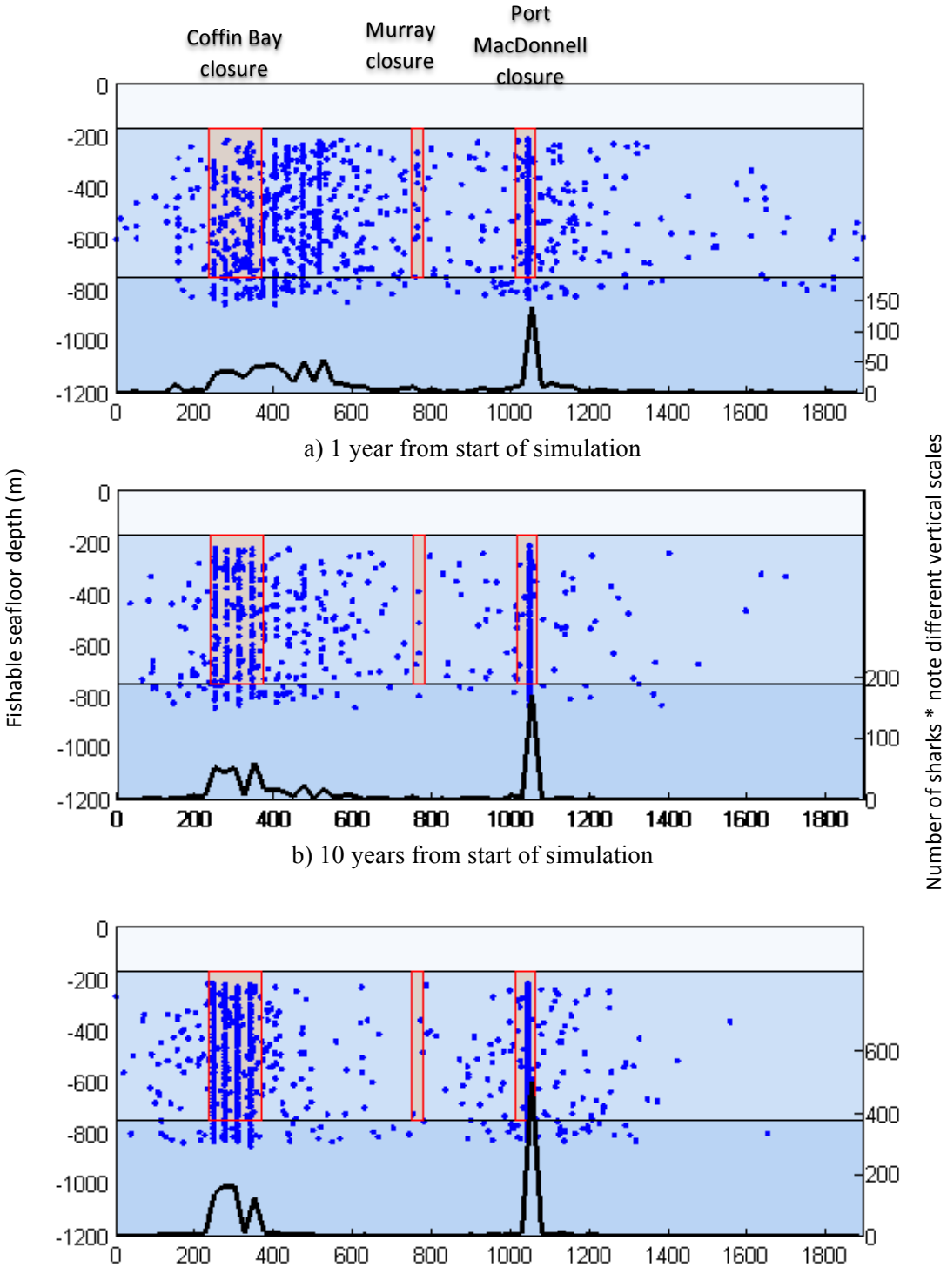


Figure 5.7 Example model output from the base case year showing sharks (blue marker) protected inside closures (orange) and the remainder exposed to different fishing mortalities. Line plot at base of axis shows density.

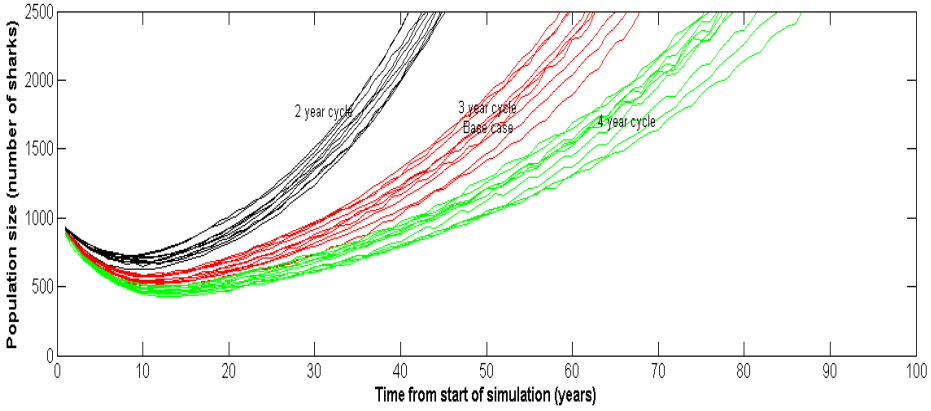


Figure 5.8 Population trend for modeled *Centrophorus zeehaani* showing sensitivity to uncertainty in the length of the female reproductive cycle. Three year (red), two year (black) and four year reproductive cycle (green).

Scenario evaluation

Three fishing scenarios were considered. The first modifies the base case to eliminate gillnetting in continental shelf waters shoreward of the 180 m contour (to protect Australian Sealions) and introduces auto-longline fishing in the same waters (to allow fishing for gummy shark to continue). In this scenario, *C. zeehaani* recovery occurred in 63.9±2.1 years, not significantly earlier than the base case (Table 5.3). This result occurs because *C. zeehaani* are constrained by the model not to enter these continental shelf waters (too shallow) (Figure 5.7) therefore fishing mortality in this zone did not affect *C. zeehaani*, regardless of the fishing method.

The second fishing scenario allows the reintroduction of trawling in mid-continental slope waters that have been closed to avoid capture of orange roughy, a protected species in Australia. Recovery under this scenario took 109±4.9 years, 45.9 years longer than the base case. This result occurred because the bathymetric distribution of *C. zeehaani* and orange roughy fishing overlapped between the 750 and 850 m bathymetric contours, causing additional fishing mortality of *C. zeehaani*. This was particularly apparent within the along-slope range of the Coffin Bay and Port MacDonnell closures, where the population became concentrated after 50 years (Figure 5.7c).

In the final fishing scenario it was assumed that handling practices on board auto-line vessels could be improved to increase the number of sharks released alive enough to halve *f*. Recovery was achieved in 62.7±2.7 years, slightly faster than the base case but not

significantly so. This result was heavily influenced by *f* trawl that continues to impact on *C. zeehaani* even when *f* auto-longline is reduced in the primary Fishing Zone 1 (Figure 5.2).

Closure scenario evaluation found that doubling or halving the size of the Coffin Bay closure, located over a concentration in *C. zeehaani* abundance, lead to significantly faster (12.5 years) or slower recovery times (12.5 years) than the base case (Table 5.3). Conversely, doubling or halving the size of the Murray closure does not significantly affect the recovery time, because abundance of *C. zeehaani* was not high there.

5.4 Discussion

This results of this study shows that simulation modeling can be used to predict the effectiveness of a spatial management network implemented for the recovery of a vulnerable deep-sea species. Clear management objectives combined with the IBM provided a quantitative estimate of the timeframe needed to achieve recovery. The base case estimate for the population to recover from its depleted level of 8% of initial numbers to 20% was 63±3.1 years.

Underlying movement ecology

This model contains some underlying ecological assumptions. Firstly, the general assumption that the life-history of *Centrophorus* responds to light or other seasonal variables that give breeding and associated movements a predictable frequency. This seems reasonable given *C. zeehaani* movements are influenced by night and day in particular and season (Daley, Williams *et al.* 2015) (Chapter 3) even though temperature and light vary much less than surface waters (Wetherbee 1996).

It is important to note that the model links success of the closure network to high residency by mature breeding females. There are two analyses that provide evidence that this is the case (Daley, Williams *et al.* 2015) (Chapter 3): Firstly linear regression showed that the number of males detected within the array declined significantly (Figure 3.2). By contrast, there was no evidence of a decline in the number of females. Secondly, coincident patterns in the movements of individual males patterns, suggest a number of males left the closure in late summer or autumn and returned in late winter or spring (Figure 3.4).

It is possible that female homing behaviour is a tradeoff between physiological needs during gestation and avoiding predators or finding food that are more likely to be priorities for males, hence higher mobility. Female *C. zeehaani* make a high maternal investment in the large pre-

ovulated follicles with similar levels of total lipid content that are similar to the maternal investment in the eggs of birds and reptiles (Pethybridge, Daley *et al.* 2011).

Inputs and sensitivity tests

This study provides a useful reminder that basic biological data are essential inputs for a reliable demographic model. Key uncertainties were length of the female breeding cycle and natural mortality. For deep-sea sharks the number of years in the female breeding cycle can be calculated from the number of size classes of embryos dissected from females collected at the same time from a population. As there were insufficient embryo data for *C. zeehaani* to calculate fecundity using this method, a three year cycle was assumed. This assumption was based on a closely related species but from a different area (Jamaican waters) (McLaughlin and Morrissey 2005). The greatest uncertainty in the model is the natural mortality estimate. This is difficult to measure but has been estimated for other shark species using relationships with the von Bertalanffy growth rate *k*, growth parameters and temperature (Forrest and Walters 2009). There are insufficient aging data to develop a reliable *k* estimate for *C. zeehaani*, particularly a lack of juveniles and individuals near maximum size (Whiteley 2008). This is disappointing, given that hundreds of tonnes of *Centrophorus* were harvested commercially in Australia (Daley, Stevens *et al.* 2002) and perhaps represents a missed opportunity to calculate biological parameters now this species is protected.

Improved spatially explicit demographic monitoring is needed to improve reliability of the assessment. The frequency of breeding females was low in proportion to mature males and immature individuals. This contributed to modeled decline in the population in the initial ten years of model runs until the proportion of breeding females increased. These data were collected from within the population range, but only a small part. This could be improved if data could be obtained non-lethally across the population range and may lead to more optimistic model results. Similarly measures of abundance were only estimated in some parts of the range because of limited survey data. It is important to note that measurement of recovery time is extremely sensitive to patchiness in abundance. The base case predicted that if the distribution of *C. zeehaani* is as patchy as the estimated distribution then the time for recovery is 31.8 years faster than with a random uniform distribution.

While not tested in this simulation, the model inputs could be improved by further field-testing of juvenile movement rates and residency. Larger adult sharks were detected more often than smaller adult sharks (Chapter 3); by extrapolation juvenile movement rates are likely to be slower than the adults simulated in the model. Juveniles could have less exposure to fishing if they stay in the closures. On the other hand, juveniles distributed in the fished

areas would be less likely to move into closures, giving them greater exposure. While these direct effects are likely to balance each other, it means the recovery time will be even more sensitive than the model predicts to correct location of closures around any nursery areas, which are not yet well mapped.

One remaining uncertainty was the 21 unexpectedly fast hourly movements. It seems unlikely that *C. zeehaani* with a body length of less than 1 m is able to sustain this rate of movement for more than 10 km between receiver curtains. It is important to note these calculations take the detection location to be at the base of receiver, whereas the detection range was up to 900m (Chapter 3). This means that the distance a shark moved between two receiver curtains could have been 1.8 km shorter than calculated, potentially leading to and overestimate of swimming speed. It doesn't seem appropriate to remove these observations from the simulation model because there is also the potential to underestimate some hourly movements.

Although sensitivity testing found this uncertainty did not significantly affect the predicted recovery time, care is needed not to assume sustained swimming speeds of > 2 km/hr. are possible for *C. zeehaani* based on this study. Refining measurements of swimming speed for *C. zeehaani* would benefit from considering alternative receiver array configurations to help eliminate the problem of over/understating swimming speed.

Scenario evaluation

Bathymetry based spatial management arrangements for orange roughy, have a substantial effect on *C. zeehaani* numbers. This is likely to be the case for protected marine species that occur within the same bathome, in this case onto the mid-slope. *Centrophorus zeehaani* is restricted mainly to the upper-slope and on average individuals move onto the mid-slope mainly at night. It would be biologically meaningful to manage *C. zeehaani* bycatch on Orange Roughy fishing grounds by restricting fishing there to daylight hours. The hourly time step of the model allows this to be explored in the future. For now such management arrangements are not practical because of gaps in of seafloor mapping data. These gaps mean the positions of the 750 and 1200 m bathymetric contours that define the mid-slope cannot yet be delineated reliably on key fishing grounds. This would make fishery compliance monitoring impractical.

Attempting a recovery plan for a deep-sea shark species over a period of some 63 years is farsighted and ambitious. The results of this study indicate that for, the case study species at least, the prospects of success are reasonable, provided estimates of natural mortality in

particular, and other biological factors are accurate. This time period is longer that individual careers and some type of succession planning will be needed. There are other species from the upper-continental slope of southern Australia that are probably just as vulnerable as *C. zeehaani* (Graham, Andrew *et al.* 2001; Walker and Gason 2007). It will be expensive and perhaps not possible to collect detailed movement data on all these species. Developing spatially explicit knowledge of abundance, size structure and sex ratios and obtaining some estimate of movement rate can be used as proxies for amenity to spatial management for these deep-sea shark species. It is important to consider spatial management for overlapping protected species, as well as the different fishing methods that affect them collectively.

CHAPTER 6 GENERAL DISCUSSION

This thesis looks in detail at the plausibility of developing conservation recovery plans for deep-sea sharks, focusing on spatial management. Two protected species from Australia are used as a case study. The work is set in the context of a clear mandate to develop a recovery strategy without sufficient supporting science. Below I review the main steps in developing the strategy, discuss some key remaining uncertainties and consider application of conservation management strategies to other deep-sea shark species.

Taxonomy, population structure, and species identification

Species composition (taxonomy) and species identification problems continue to hamper effective management of the effects of fishing on deep-sea sharks. Leading examples are species from the genera *Centrophorus* and *Squalus*, particularly those from the upper-slope bathome where latitudinal variation in environment leads to higher endemism than the more uniform conditions on the mid-slope.

My genetic study of genus *Centrophorus* in Australia using the 16S gene (Daley, Appleyard *et al.* 2012) (Chapter 2) supports the findings of previous morphological studies in Australia (White, Ebert *et al.* 2008) that identified a number of Australian and regional endemic species. A subsequent genetic study using the NADH2 gene found *C. zeehaani* genetically matched to *C. Squamosus* from the Atlantic (Naylor, Caira *et al.* 2012), suggesting *C. zeehaani* could be a synonym of *C. Squamosus.* In this thesis and in other studies no single marker was able to identify all valid species of *Centrophorus*. The 16 S marker developed in Chapter 1 has subsequently been used in a review of North Atlantic *Centrophorus* (Verissimo, Cotton *et al.* 2014). That study classified different putative species to different clades using the 16S and Co1 genes, highlighting a problem with relying on any one gene for genetic taxonomy. A simple solution is to develop and use a combination of markers. Future genetic taxonomy studies could apply the 16S and other genes to the genus *Squalus,* particularly to *S. 'mitsukurii',* a name that has been applied to a number of confused species (Cotton 2010).

At finer geographic scales, genetic studies aim to delineate populations as management units. In the case study, the USDMS (Upper-Slope Dogfish Management Strategy) for *C. zeehaani* and *C. harrissoni* included genetic diversity as an objective. This objective adds resilience to the strategy by including multiple populations of both *C. zeehaani* and *C. harrissoni* in different closures. This will help conserve these species even if a localised extinction of one population occurs during the recovery period. Such resilience is important because, given the

length of the recovery period, it is not only fishing that could impact on populations. Other possible causes could include a localised anthropogenic accident, such as an oil spill, or the effects of ocean warming. Guarding against these potential negative effects also requires an understanding of the distribution of populations.

The number of populations and their geographic distributions was the leading uncertainty in the development of management strategies for the case study species (Chapter 4.2). Initially I considered genetic population studies to address this uncertainty but I was unable to collect sufficient samples of *C. harrissoni* and *C. zeehaani* during the time available for this study. More importantly, delaying the management response to wait for more genetic studies would have lead to further depletion due to bycatch in fisheries that could have been irreversible, therefore an alternative method was needed to map populations.

I used the spatial scale of segregation between different demographic components (males, females and juveniles) to map inferred population distributions of *C. zeehaani* and *C. harrissoni* (Chapter 4). I based this method on the biological principle that males, females and juveniles in a viable shark population must meet to mate, pup, and recruit. I lead research voyages to collect the supporting demographic data along the south and east coasts of Australia from 2005–2010. Analyses of these data indicated restricted population distributions on the upper-slope. Subsequently, in a co-authored publication, we explored the broader utility of demographic approaches for three other deep-sea shark species with different ecologies (Moura, Jones *et al.* 2014). Results indicated large-scale demographic segregation and movements across the Atlantic, Indian and Pacific Ocean basins providing a stark contrast with the restricted distribution of *C. zeehaani*. It is therefore important to collect species-specific baseline demographic data. Further, ongoing monitoring is needed to determine if these patterns are stable over time.

Effective ongoing monitoring of deep-sea shark populations needs to be species specific. Most fisheries rely on commercial catch data, which is not always resolved to species and difficult to verify because many species are morphologically similar, therefore independent surveys will be needed.

Life history

The population assessment of *C. zeehaani* in this study and the management responses were underpinned by key parameters of basic biology including fecundity and natural mortality (*m*). Both were key uncertainties in predicting the timeframe for recovery (Chapter 5). Co-authored publications contributed to the best possible estimates for both parameters.

Fecundity is the product of litter size and the length of the female cycle. Litter size was determined from the number of embryos in *C. zeehaani* (Graham and Daley 2011). Breeding frequency remains more difficult to determine. For shallow water shark species, breeding seasons can be determined from seasonal changes in the size of embryos or condition of the ovary (Awruch, Pankhurst *et al.* 2009; Hamlett and Koob 1999). In the deep-sea these methods are generally not effective where the varying light signals that drive seasonal cycles in shallow waters are much weaker. An alternative approach is to calculate the length of the female cycle from the number of embryos in different size classes sampled at different times (Rochowski, Graham *et al.* 2015). The key-limiting factor for this method is that it requires dissection of many pregnant females. I therefore had to base my estimate of cycle length on *C. squamosus*, from the Atlantic (McLaughlin and Morrissey 2005) where environmental conditions that influence reproduction and growth differ from Australian waters.

Natural mortality (*m*) was the most difficult biological input to determine. A precise estimate of *m* generally requires monitoring changes in the number of individuals in different age classes of a population over long time series, generally tens of years (Leslie 1945). Cost and logistical problems preclude this approach for rare deep-sea sharks. Here we based the estimate on 0.42 *k* (growth parameter of the von Bertalanffy growth model), a ratio averaged across a range of shark species (Forrest and Walters 2009). This method was considered the most appropriate as *k* is strongly related to growth (Forrest and Walters 2009). I used a *k* value obtained for *Deania calcea*, a closely related species from the same family (Centrophoridae) (Irvine, Daley *et al.* 2012) because of limited age data for *C. zeehaani*, particularly juveniles (Whiteley 2008).

Estimating key biological parameters in the case study was not entirely satisfactory but essential because *C. zeehaani* was already too depleted to dissect more samples for ageing and reproduction data. This highlights a need for other studies, where possible, to collect basic life history data for deep-sea sharks, particularly for common bycatch species that can be sampled readily from commercial catches, before those populations become overfished. The implication for management is this needs to be done early during the development of fisheries. A partial solution is to make biological sampling a requirement during the development of new fisheries or expansion of existing fisheries into new areas.

Home range and movement ecology

Minimising capture stress and mortality was an essential precursor to measuring home range and movements using telemetry. This involved managing the effects of temperature and pressure changes during capture from the deep-sea. *Centrophorus zeehaani* and *C.*

squamosus are particularly vulnerable to capture stress, whereas other deep-sea sharks such as *Squalus cubensis* are much less so (Daley, Williams *et al.* 2015; Talwar 2017). The reasons for these differences are unknown. Importantly for future tagging studies I found that stress was minimised and mortality was eliminated when individuals were captured using hook and line in cool dark conditions then released at the surface as quickly as possible. An alterative release method was trialed in this study and one other (Talwar 2017). *Centrophorus zeehaani* and *C. squamosus* individuals were lowered to the seafloor in cages to avoid predation but in both cases mortality resulted from use of the cage.

My studies of movement ecology using passive acoustic telemetry were primarily pragmatic in design, intended to help match the scale of closures to the home range of *C. zeehaani*. Sampling focused on mature females because their number limits breeding success of the population. This is particularly important for *C. zeehaani* population dynamics because females that have only one pup at a time (Chapter 5). The extent that females give birth at the same location year after year is a focus for the study of inshore shark species (Hernández, Daley *et al.* 2015) but for deep-sea sharks this was virtually unknown. Given that the upper-slope is only a few km wide off southern Australia (AFMA 2012) along-slope movements were the primary indicator of home range area. Female residency was best demonstrated using the simple index of abundance on a monthly scale. My along-slope linear model (GAMM) showed most *C. zeehaani* individuals remained near their release point year round, indicating residency within a small along-slope range. By contrast subsequent studies have shown that *C. squamosus,* a closely related species from the Atlantic, undertakes much larger scale (>1000 km) migrations (Rodríguez-Cabello, González-Pola *et al.* 2016). This shows movement ecologies differ between even closely related deep-sea shark species.

The across-slope linear (GAMM) model provided additional insights into spatial management as well as insights into the movement ecology of upper-slope sharks and their role in the upper-slope community. *Centrophorus zeehaani* consistently moved into shallow waters at night, therefore nighttime closures of shallow waters would be biologically meaningful. At this stage however depth closures are not practical because the cost of analysing fishing vessel monitoring data on an hourly timescale would be prohibitive and a lack of detailed seafloor mapping data. The across slope GAMM also provided insights into the diurnal ecology of *C. zeehaani*. The results indicate diurnal movements of *C. zeehaani* are part of a specialised feeding strategy, closely tuned to the movements of mid-water prey species. This is consistent with diet studies that found mid-water species prevalent in the diet of *C. harrissoni* and *C. zeehaani* (Daley, Stevens *et al.* 2002).

It is useful to consider how acoustic tracking could be refined for ecological applications, including habitat use and community ecology. An interesting finding for the *C. zeehaani* population that emerged from the individual based model (Chapter 5) was how sensitive the relationship between closure location and recovery time was to individual patchiness. Assuming individual patchiness is due to habitat patchiness, further exploration of fine scale habitat use could have practical benefits for spatial management. This would require an acoustic receiver array with much closer spacing than an array optimized to test residency. Regardless of the intended application, it remains essential to consider sample size. The results from the (GAMM) linear models of movement (Chapter 3) found that individual variation contributed more to variation in movement across-slope than any other factor for *C. zeehaani*. Although female residency was a key focus of this study, only 13 could be tagged. This was an adequate sample size to contrast sex-based residency using the simple metrics but not adequate for detecting the underlying causes using the GAMM framework. This means that higher sample sizes will be needed to drive ecological models.

Fishery management and conservation planning

The management strategy evaluation (MSE) approach I developed in this thesis (Chapter 4) was a turning point in moving towards a recovery plan for *Centrophorus* spp., simply because it moved away from attempts to provide the type of concise and unambiguous recommendations managers generally rely on. Conversely, natural resource management is fraught with uncertainty. There are no unique solutions because society values the competing objectives of both resource use and conservation. Contemporary papers point to the need for multi-disciplined approaches to resolve complex issues of environment, law, policy and economics (Thébaud, Link *et al.* 2017). The MSE approach used here takes a small but important step in improving communication across these areas.

I modified the MSE approach already used in fisheries to explore the consequences of alternative management restrictions, mainly for target species in fisheries (Smith, Fulton *et al.* 2007) and subsequently for managing recreational fisheries in reserves (Thébaud, Ellis *et al.* 2014). The main differences are that my approach here is semi-quantitative and deals with conflicting objectives. The guiding principles are to apply the following steps in order: identify objectives; consider existing knowledge; identify criteria to measure performance; choose options at different scales; and predict the performance of each option. The example presented in Chapter 4 explains these aspects in detail highlighting potential application to spatial management of other vulnerable marine species.

The selection of objectives and corresponding criteria is the most critical aspect of the process. The corresponding criteria are deliberately not weighted explicitly as this avoids a value judgment on competing objectives. Conservation criteria need to be as precise as existing knowledge permits. In this study, compiling existing knowledge was the role of the expert group but stakeholders contributed to criteria selection. Overall the conservation criteria were the simplest to develop. The competing economic criteria used here were simplistic, partly because the catch data were not available for some jurisdictions. A useful extension of the approach would be refining the economic criteria to include profit analysis and understanding the net economic effect of geographically displaced effort in the fishery.

Surprisingly there was general agreement on the scoring of the options among stakeholders despite conflicting economic and conservation objectives. It was only the implicit weighting of these objectives that was contentious. The final choice of options implemented using the method was a management decision that represented a trade-off between resource use and conservation with associated risks to both objectives.

Implementation and monitoring conservation

Species conservation plans are most likely to be supported, and funded, if they contain performance targets that are quantitative and time constrained. A gap remains between this ideal and most real world examples because of poorly defined performance targets and/or scientific uncertainty. In Chapter 5, I synthesise key findings from the preceding chapters to offer an example of how this gap can be closed. The example is modeled at the population level, (central population of *C. zeehaani*) under the current management strategy (large permanent closures and other areas opened to different fishing methods). Predictions are obtained from an individual based simulation model. An essential precursor to a quantitative performance measure is a quantitative objective. A recovery from 8% to 20% of initial biomass (represented in the model as individual shark numbers) was chosen for the case study.

Key inputs for the simulation model were: geographic distribution of the population defined by demographics (Chapter 4); life history of the population (co-authored publications); movement ecology (Chapter 3); and spatial management arrangements (Chapter 4). The key output was the time taken for recovery, which was 63 years in the base case. Sensitivity tests found the greatest uncertainties were gaps in basic biological knowledge. This highlights the need for basic research.

During the recovery period there will be changes of government and policy and institutions may come and go. Most certainly priorities will change and the management of other deep-sea species will interact with the management of deep-sea sharks. The simulation approach allows managers, scientists and stakeholders to test alternative objectives and management strategies in the model. Ongoing field monitoring is needed to ground-truth the simulated predictions. This should include abundance and demographic stability inside and outside the closure. Cost effective monitoring can be achieved using fishery observers outside closures but independent surveys will be needed inside. The main disadvantage of catch and effort methods for monitoring is the resulting mortality of some of the protected *Centrophorus* species. This can be minimised by fast release of captured individuals from the surface (Chapter 3). The only alternative survey method with zero mortality tested to date on *C. zeehaani* and *C. harrissoni* is baited underwater video cameras. A trial found this method was able to identify *Centrophorus* species but could not count individuals reliably (McLean, Green *et al.* 2015).

Conclusions

This thesis stands out from other contemporary treatments of deep-sea shark conservation by moving beyond assessing impacts and collecting background biological data to developing a cohesive recovery strategy and supporting its ongoing implementation and monitoring. Key contributions to the field are firstly, the first detailed passive acoustic telemetry study of movement ecology in the deep-sea; secondly, an MSE approach used to support communication and understanding of spatial management options; and finally, a simulation modeling approach to test the effects of alternative closed areas and fishing restrictions on conservation outcomes across the range of a population and a closure network. I also contributed to filling key knowledge gaps in biology and population structure and developed methods to estimate some parameters from related species where rare species could not be sampled. Only time will tell if the case study species are conserved but this work makes a unique and compelling argument that effective conservation strategies can be developed for deep-sea sharks, albeit at substantial economic cost.

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APPENDIX I. SUPPLEMENTARY TAGGGING DATA SUMMARIES

Supplementary Table A. Details of release locations and individual summary metrics for individual *Centrophorus zeehaani* (13 females and 58 males) released and detected at acoustic receiver curtains deployed on the upper-continental slope of Southern Australia.

ID	Tag Date	Sex	TL (cm)	Release Location	N Days	DUR (days)	MLD (km)	DI	Release Depth (m)
805	12/08/9	F	102	West	3	70	2	0.01	635
807	12/08/9	F	103	West	36	479	17.3	0.08	635
804	12/08/9	F	112	West	67	481	15.3	0.15	635
806	12/08/9	F	104	West	111	482	15.3	0.25	635
810	12/08/9	F	104	West	55	483	56.7	0.12	635
808	12/08/9	F	101	West	107	485	15.3	0.24	635
812	12/08/9	F	103	West	120	485	15.3	0.27	635
740	12/08/9	M	92	West	0	0		0	635
809	12/08/9	M	92	West	0	0		0	635
738	12/08/9	M	93	West	14	118	30.6	0.03	635
813	12/08/9	M	90	West	113	479	36.5	0.25	635
733	12/08/9	M	89	West	199	483	30.6	0.45	635
743	12/08/9	M	87	West	77	484	36.5	0.17	635
744	12/08/9	M	92	West	256	484	15.3	0.57	635
811	12/08/9	M	92	West	150	485	15.3	0.34	635
734	11/08/9	F	96	Central	11	393	43	0.02	444
742	11/08/9	M	90	Central	54	129	14.6	0.12	444
745	11/08/9	M	88	Central	59	480	14.6	0.13	444
732	11/08/9	M	88	Central	101	481	55.6	0.23	444
730	11/08/9	M	89	Central	71	486	52.9	0.16	444
747	11/08/9	M	86	Central	284	486	14.6	0.63	444
288	9/08/9	M	90	C-East	41	178	19.0	0.11	500
768	9/08/9	F	97	East	0	0		0	490
795	9/08/9	F	91	East	0	0		0	490
772	9/08/9	F	104	East	26	124	56.3	0.06	490
771	9/08/9	M	87.5	East	0	0		0	490
774	9/08/9	M	88.5	East	0	0		0	490
776	9/08/9	M	91.5	East	0	0		0	490
778	9/08/9	M	91	East	0	0		0	490
790	9/08/9	M	90	East	0	0		0	490
773	9/08/9	M	93	East	1	30	na	0	490
791	9/08/9	M	87	East	13	121	53.7	0.03	490
777	9/08/9	M	90	East	4	123	2	0.01	490
788	9/08/9	M	86.5	East	7	123	2	0.02	490
775	9/08/9	M	93	East	39	124	37	0.09	490
796	9/08/9	M	89	East	42	171	56.3	0.09	490
781	9/08/9	M	89	East	13	360	21.3	0.03	490
769	9/08/9	M	99	East	10	442	21.3	0.02	490
789	9/08/9	M	88.5	East	42	449	21.3	0.09	490
784	9/08/9	M	89.5	East	13	455	2	0.03	490
800	9/08/9	M	95.5	East	4	456	21.3	0.01	490
802	9/08/9	M	91	East	7	457	2	0.02	490
793	9/08/9	M	92	East	48	458	21.3	0.11	490
736	9/08/9	M	92	East	65	479	58.3	0.14	490
779	9/08/9	M	90	East	43	479	37	0.1	490
798	9/08/9	M	90.5	East	99	480	2	0.22	490
770	9/08/9	M	93	East	47	482	2	0.1	490
803	9/08/9	M	85	East	86	482	37	0.19	490
737	9/08/9	M	89	East	105	483	75	0.23	490

Supplementary Table A. (Continued)

ID	Tag Date	Sex	TL (cm)	Location	N Days	DUR (days)	MLD (km)	DI	Release Depth (m)
782	9/08/9	M	90	East	90	483	56.3	0.2	490
783	9/08/9	M	91	East	14	484	53.7	0.03	490
799	9/08/9	M	94	East	57	484	2	0.13	490
801	9/08/9	M	86.5	East	78	484	21.3	0.17	490
786	9/08/9	M	86	East	147	486	21.3	0.33	490
787	9/08/9	M	90.5	East	83	487	21.3	0.18	490
780	9/08/9	M	90	East	36	488	56.3	0.08	490
785	9/08/9	M	90	East	294	488	37	0.65	490
792	9/08/9	M	92	East	260	488	56.3	0.58	490
794	9/08/9	M	90.5	East	233	488	2	0.52	490
797	9/08/9	M	91	East	149	488	2	0.33	490
749	10/08/9	F	102	Canyon	12	485	43.3	0.03	386
748	10/08/9	F	102	Canyon	102	486	52.5	0.23	386
756	10/08/9	M	102	Canyon	1	59	na	0	386
757	10/08/9	M	102	Canyon	1	6	22.3	0	386
746	10/08/9	M	102	Canyon	9	443	59	0.02	386
750	10/08/9	M	102	Canyon	65	480	22.3	0.14	386
755	10/08/9	M	102	Canyon	29	481	22.3	0.06	386
753	10/08/9	M	102	Canyon	81	482	34	0.18	386
754	10/08/9	M	102	Canyon	71	482	43.3	0.16	386
751	10/08/9	M	102	Canyon	107	485	56.5	0.24	386
752	10/08/9	M	102	Canyon	162	487	22.3	0.36	386

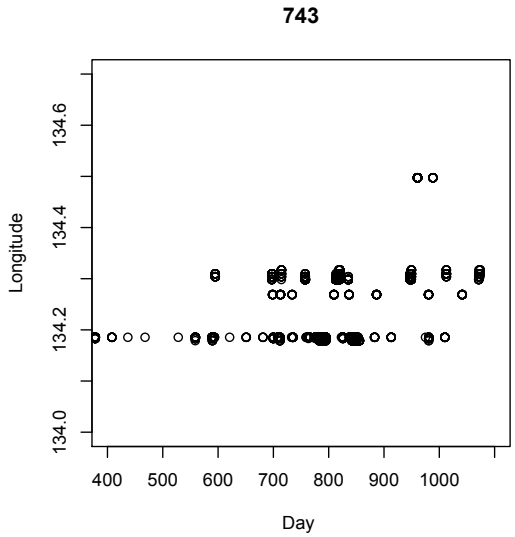
ID = transmitter identity; TL = total length; Location = Tagging location (see Figure 1); N Days = total number of days with a detection anywhere within the array; DUR = duration between date of tagging and the last day detected; MLD = minimum liner dispersal or distance between two furthest receivers with detections; RI = residency index (daily); na are sharks with just a single detection and these omitted from analysis as they may be spurious.

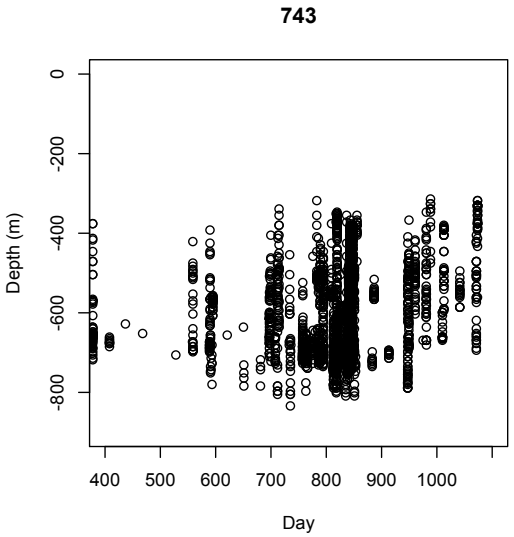
Supplementary Table B. Summary metrics of individual residency within a fishery closure for tagged *Centrophorus zeehaani* (13 females and 58 males) off southern Australia. Effects of sex, release location, habitat and total length (P-values from analysis of variance tests of the influence of biological factors and habitat on summary metrics, with significant difference in bold).

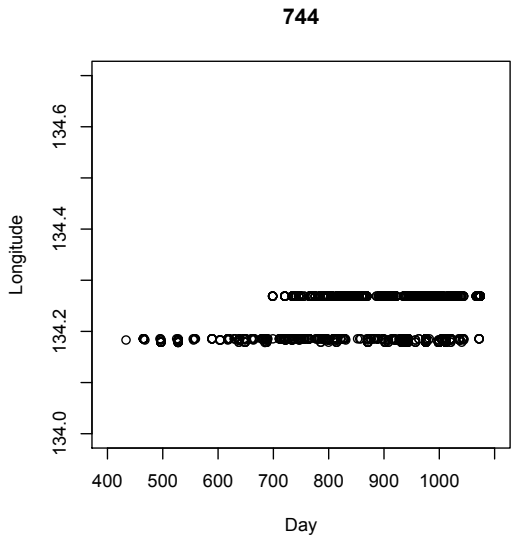
Summary metric	Mean	SE[(a)]	P: Sex	P: Release point	P: Release habitat	P: Total Length
Number of days	78.0	9.6	0.349	0.422	0.213	**0.0345**
Duration (days)	408	19	0.955	0.639	0.801	0.082
Daily Detection index (Days detected/days at liberty)	0.174	0.02	0.361	0.407	0.521	0.206
Maximum Linear Distance (km)	19.9	2.6	0.813	0.492	0.238	0.444

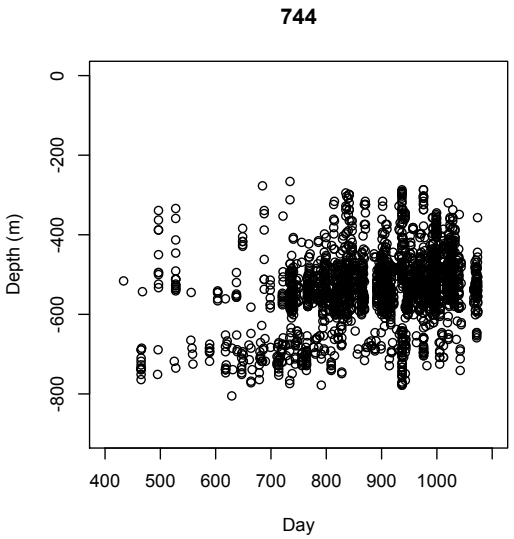
(a) Standard error.

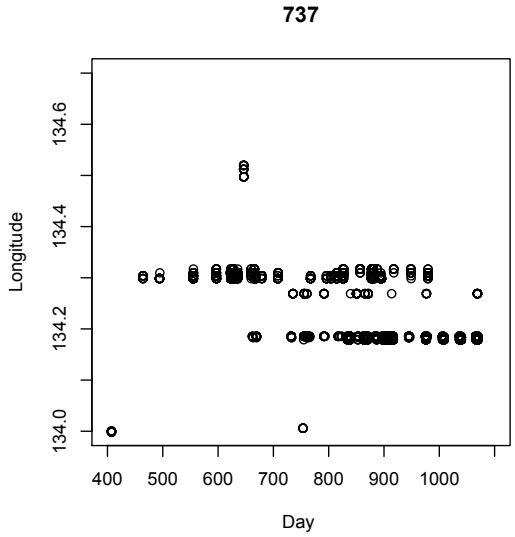
APPENDIX II. EXAMPLE TRACKING DATA FOR *C. zeehaani*







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Longitude
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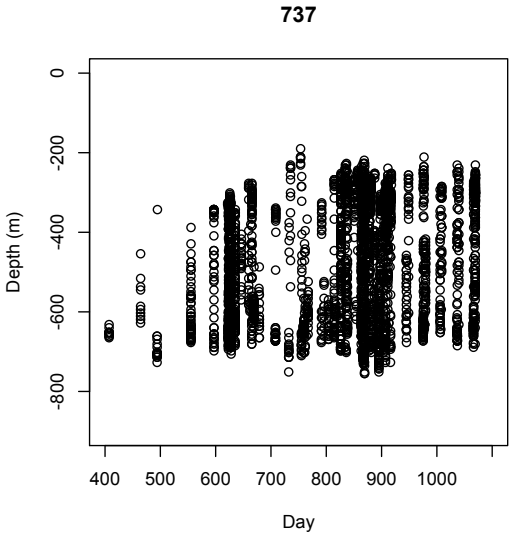
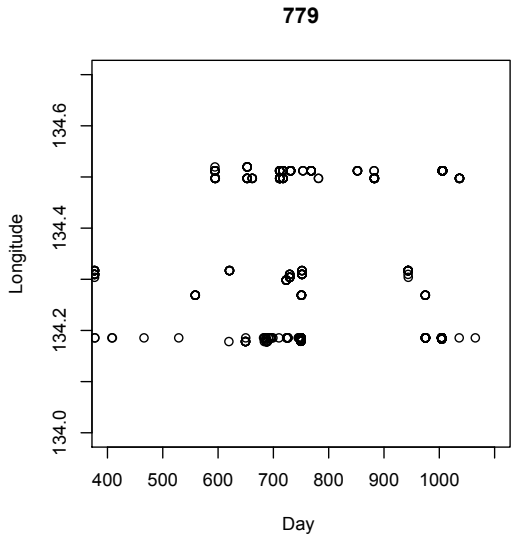
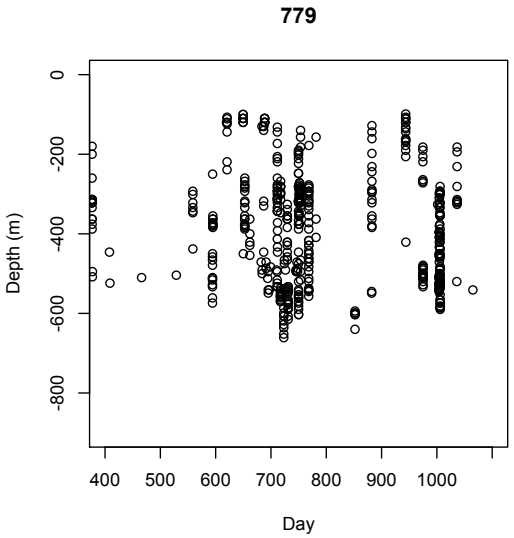
134.2
134.4
134.6
400
500
600
700
800
900
1000
Day


737
Depth (m)
0
-200
-400
-600
-800
400
500
600
700
800
900
1000
Day


779
Longitude
134.0
134.2
134.4
134.6
400
500
600
700
800
900
1000
Day


779
Depth (m)
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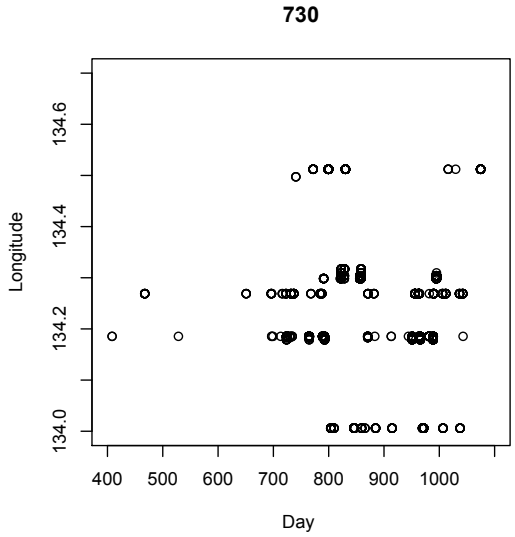
-200
-400
-600
-800
400
500
600
700
800
900
1000
Day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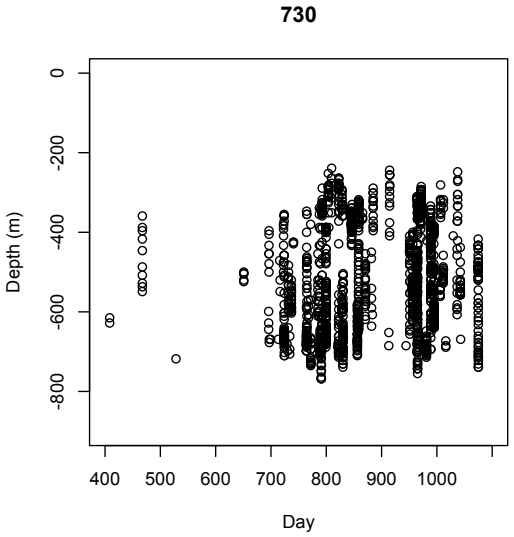
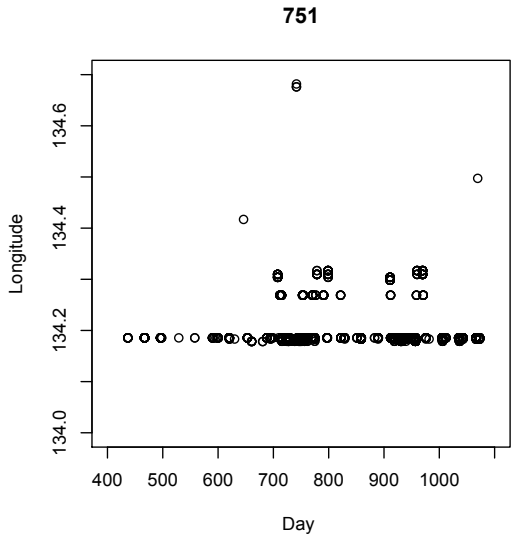
Longitude
134.0
134.2
134.4
134.6
400
500
600
700
800
900
1000
Day


730
Depth (m)
0
-200
-400
-600
-800
400
500
600
700
800
900
1000
Day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Longitude
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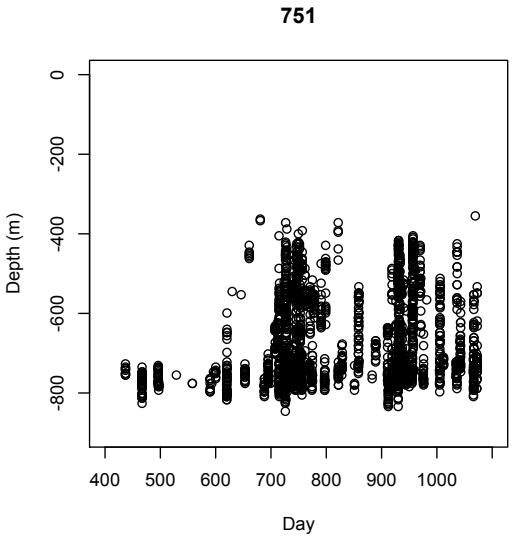
134.6
400
500
600
700
800
900
1000
Day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Depth (m)
0
-200
-400
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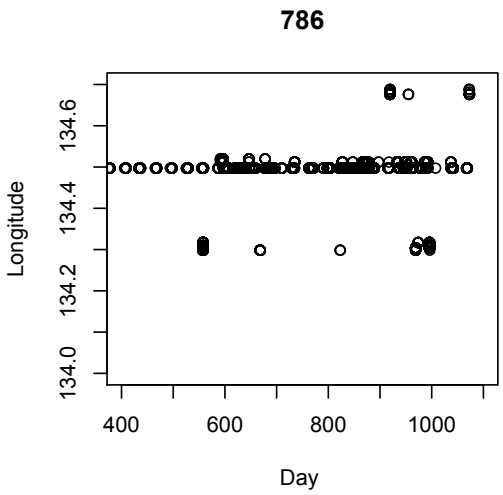
-800
400
500
600
700
800
900
1000
Day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Longitude
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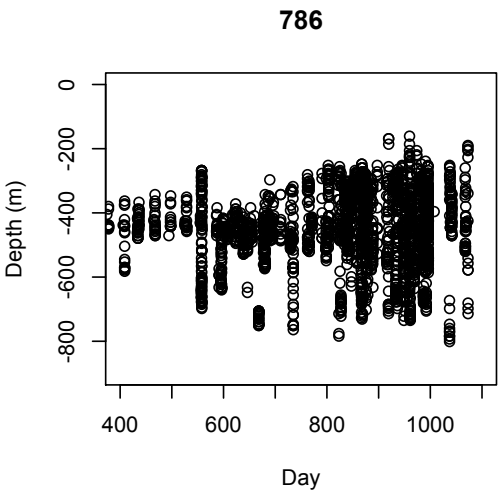
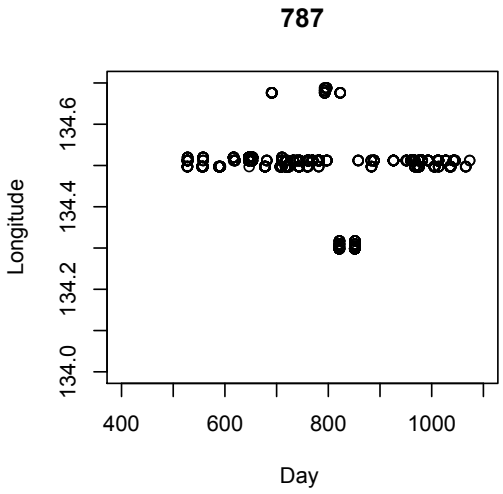
134.2
134.4
134.6
400
600
800
1000
Day


786
Depth (m)
-800
-600
-400
-200
0
400
600
800
1000
Day


787
Longitude
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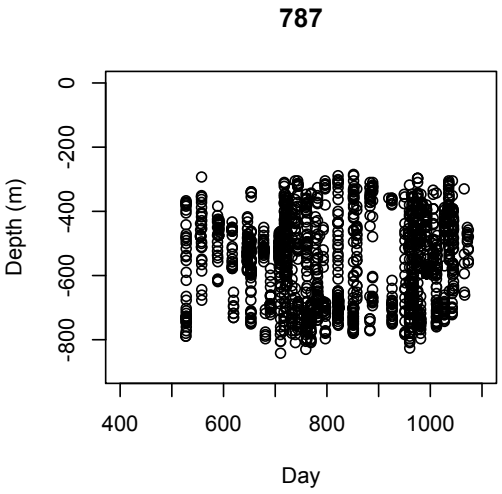
134.2
134.4
134.6
400
600
800
1000
Day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Depth (m)
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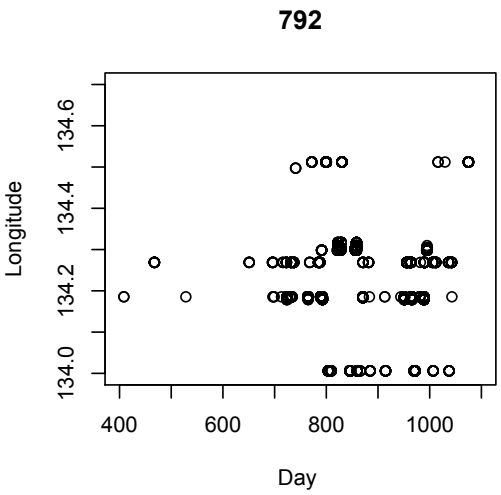
-600
-400
-200
0
400
600
800
1000
Day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Longitude
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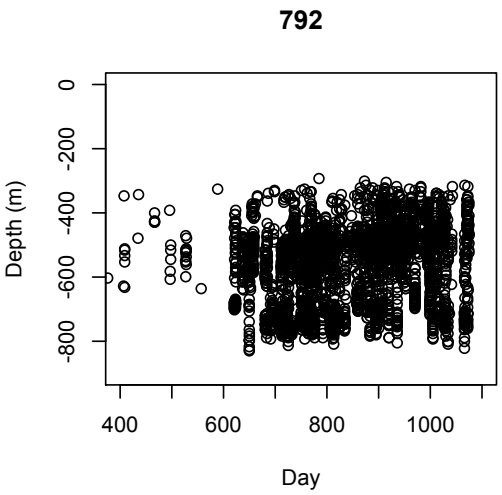
134.4
134.6
400
600
800
1000
Day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Depth (m)
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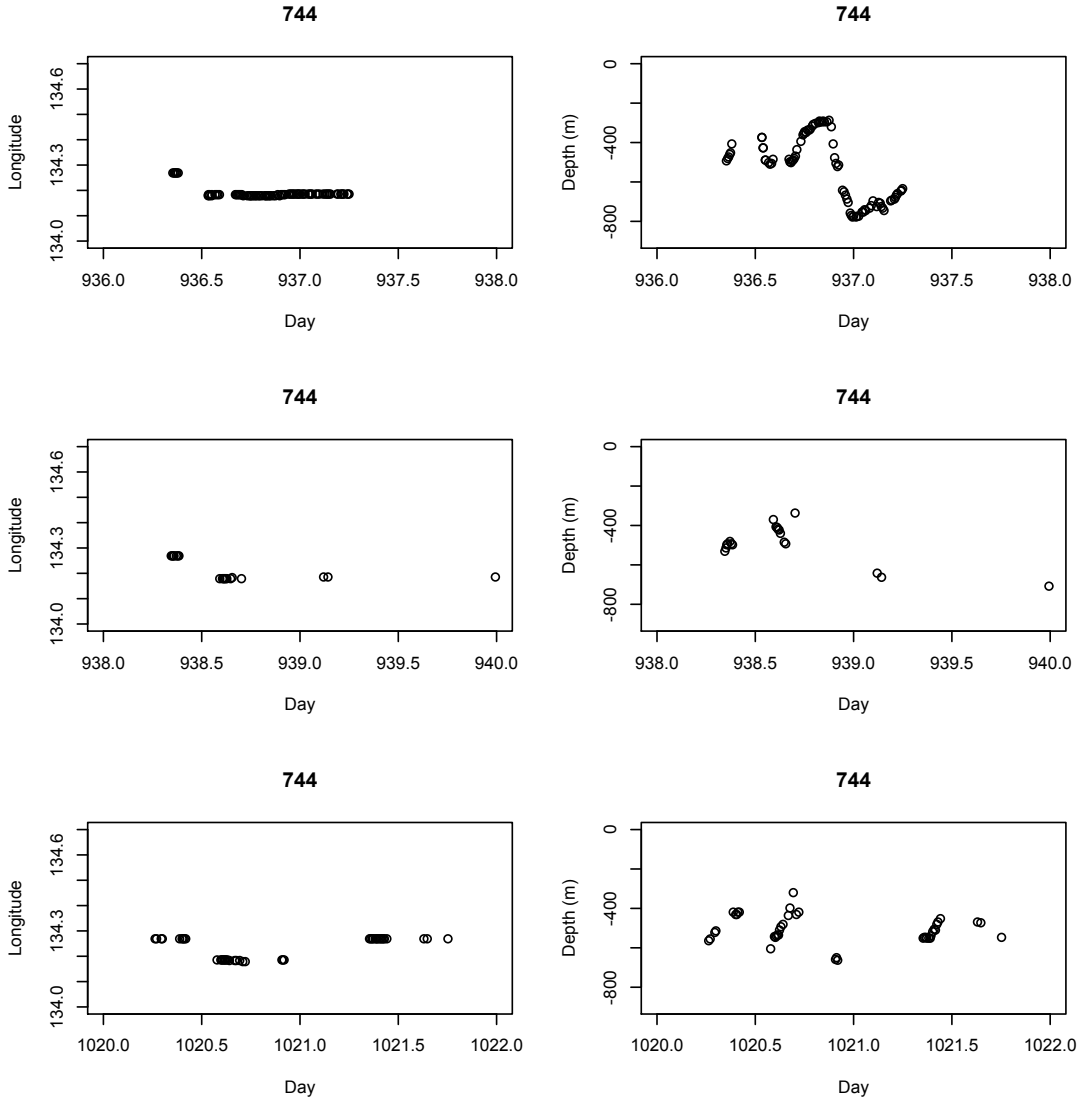
-600
-400
-200
0
400
600
800
1000
Day


744
Longitude
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134.3
134.6
936.0
936.5
937.0
937.5
938.0
Day
744
Depth (m)
0
-400
-800
936.0
936.5
937.0
937.5
938.0
Day
744
Longitude
134.0
134.3
134.6
938.0
938.5
939.0
939.5
940.0
Day
744
Depth (m)
0
-400
-800
938.0
938.5
939.0
939.5
940.0
Day
744
Longitude
134.0
134.3
134.6
1020.0
1020.5
1021.0
1021.5
1022.0
Day
744
Depth (m)
0
-400
-800
1020.0
1020.5
1021.0
1021.5
1022.0
Day